1490
Biology Human a

BIOLOGY:

THE HUMAN APPROACH

BY

CLAUDE A. VILLEE

HARVARD UNIVERSITY

CENTRAL FOOD TECHNOLOGICAL RESEARCH INSTITUTE
16 APR 1951
LIBRARY
* MYSORE. *

W. B. SAUNDERS COMPANY

PHILADELPHIA AND LONDON

1950

CFTRI-MYSORE
1490
Biology: Human a.

COPYRIGHT, 1950, BY W. B. SAUNDERS COMPANY

COPYRIGHT UNDER THE INTERNATIONAL COPYRIGHT UNION

All rights reserved. This book is protected by copyright. No part of it may be duplicated or reproduced in any manner without written permission from the publisher. Made in the United States of America at the Press of W. B. Saunders Company, Philadelphia.

REPRINTED SEPTEMBER, 1950

PREFACE

THERE can be no doubt that the concept of evolution is the major unifying force in biological thought and that in a biology text emphasis on evolution is necessary to provide a frame for, and to give meaning to, the details of structure and function. All animals and plants have had to solve the same problems of growth, reproduction, respiration, excretion, the obtaining and release of energy, and so on. Frequently, during the evolution of the various groups of plants and animals, the solving of one of these problems has caused changes in the systems providing for one or more of the other necessities of life. Thus an evolutionary and comparative treatment of the facts of biology is a great help in understanding the details of structure and function in any single organism such as man.

In this book, which is the outgrowth of the author's experience in teaching a course in Human Biology at the University of North Carolina, emphasis has been placed on the comparative and evolutionary aspects of biology and on the physiological and chemical facets of life, for the parts of biology most interesting to a beginning student, and most useful as part of a general education, are those that explain how organisms, particularly human beings, function, and how they came to be that way. In any elementary text it is sometimes difficult to steer a course between the Scylla of superficiality and the Charybdis of detailed facts. Since I believe superficiality to be the greater danger, I have tried to present, without overloading the student with facts, the information he should acquire in a college course in biology. Most students find the facts of life so interesting that a superficial treatment is both unnecessary and an affront to their intelligence.

I would like to acknowledge the advice and suggestions of my colleagues at Chapel Hill, Drs. D. P. Costello, C. S. Jones and I. C. Kitchin, who helped in organizing the Human Biology course. The primary inspiration for that course and for this book was derived from the Zoology 10 course at the University of California, taught by Dr. R. M. Eakin, whom the author had the privilege of assisting while he was a graduate student. I am indebted to Dr. Eakin and to Dr. Ralph Smith, who read parts of the manuscript and made a number of valuable suggestions.

My thanks are due the artists, Margaret Croup, Betsy Hulbert and Muriel McLatchie, who transformed my rough sketches into finished line drawings, and to Mr. Eric Mose for preparation of the end sheets. I am grateful for the help of a number of scientists—Drs. John Bonner, Lewis Dexter, William R. Duryee, R. F. Escamilla, Samuel Granick, C. A. Knight, H. Lisser, E. Perry McCullagh, J. H. McGregor, John A. McIntosh, C. F. Robinow, George W. Thorn and Chester L. Yntema—who furnished me with original photographs to use as illustrations. The American Museum of Natural History, Australian News and Informa-

tion Bureau, Chicago Natural History Museum, General Biological Supply House, San Diego Zoo, E. R. Squibb and Company, The Upjohn Company, and the United States Department of Agriculture have kindly permitted me to use certain of their copyrighted photographs. A number of publishers have granted permission to reproduce illustrations from their publications; for this I am deeply grateful to the Macmillan Company, John Wiley and Sons, Henry Holt and Company, the University of Chicago Press, Alfred A. Knopf, the J. B. Lippincott Company, the Cambridge University Press, the Blakiston Company, Harper and Brothers, Williams and Wilkins, the University of California Press, MeGraw-Hill Book Company, and the Open Court Publishing Company. I am espeeially grateful to the W. B. Saunders Company, who have allowed me to reproduce illustrations from a number of their books and who have cooperated in every way during the preparation of this manuscript. Finally, words cannot express adequately my debt to my wife, Ann Villee, who has helped with every stage of the planning, writing, editing, and proofreading of the manuscript, and without whose help this would never have been written.

In writing a general biology I have had to discuss many topics about which I have no first hand knowledge; I hope my colleagues will bring to my attention any errors which may be present in the text.

C. A. Villee

Boston, Massachusetts

CONTENTS

1. INTRODUCTION 1

Part I. BASIC STRUCTURES AND FUNCTIONS

2. PHYSICOCHEMICAL BACKGROUND 9

The Metric System 9
The Basic Material of the Universe 10
THE STRUCTURE OF MATTER 10
TYPES OF SUBSTANCES 12
CHEMICAL REACTIONS 14
ENERGY 15
TYPES OF MIXTURES 15
THE MOTION OF MOLECULES 16
MEMBRANES 18

3. PROTOPLASM 21

Physical Characteristics of Protoplasm 21
Chemical Composition of Protoplasm 21
ELEMENTS 21
COMPOUNDS 22
ORGANIC COMPOUNDS 23
Characteristics of Living Things 28
METABOLISM 29
CATALYSIS 29
MOVEMENT 30
GROWTH 30
REPRODUCTION 31
ADAPTATION 31
SPECIFIC ORGANIZATION 33

4. CELLS AND TISSUES 34

Cells 34
Animal Tissues 38
EPITHELIAL TISSUES 38
CONNECTIVE TISSUE 40
MUSCULAR TISSUES 42
VASCULAR TISSUES 42
NERVOUS TISSUE 42
REPRODUCTIVE TISSUE 43

Plant Tissues 44
MERISTEMATIC TISSUE 44
PROTECTIVE TISSUE 44
FUNDAMENTAL TISSUES 44
Organ Systems 47
Body Plan and Symmetry 47

Part II. THE VARIETY OF LIFE

5. THE PLANT KINGDOM 51

PLANT NUTRITION 51
PHOTOSYNTHESIS 52
PLANT RESPIRATION 56
PLANT DIGESTION AND CIRCULATION 57
PLANT COORDINATION 57
PLANT EXCRETION 59
Types of Plants 59
THALLOPHYTA 60
THE CONQUEST OF LAND BY PLANTS 66
BRYOPHYTA 66
PTERIDOPHYTA 69
SPERMATOPHYTA 71

6. THE STRUCTURE AND FUNCTIONS OF A SEED PLANT 78

The Root and Its Functions 78
The Stem and Its Functions 81
The Leaf and Its Functions 86
TRANSPIRATION 88
The Storage of Food 89
The Economic Importance of Plants 89

7. THE ANIMAL KINGDOM 90

The Basis for Animal Classification 92
The Protoplasmic Level of Organization 93
THE PHYLUM PROTOZOA 93
The Cellular Level of Organization 96
THE PORIFERA OR SPONGES 96
The Tissue Level of Organization 97
THE COELENTERATA 97
The Organ Level of Organization 100
THE PLATYHELMINTHES OR FLATWORMS 100
The Organ System Level of Organization 103
THE NEMERTEA OR PROBOSCIS WORMS 103
THE ROTIFERA 105
THE GASTROTRICHA 105
THE BRYOZOA 105

THE BRACHIOPODA . . . 106
THE ANNELIDA . . . 106
THE ARTHROPODA . . . 109
THE MOLLUSCA . . . 113
THE ECHINODERMATA . . . 115
THE CHORDATA . . . 118

Part III. THE ORGANIZATION OF THE BODY

8. THE BLOOD . . . 125

Plasma . . . 125
PLANT SAP . . . 127
Formed Elements of the Blood . . . 127
RED CORPUSCLES . . . 127
HEMOGLOBIN AND THE TRANSPORT OF OXYGEN . . . 128
LIFE HISTORY OF RED CELLS . . . 129
OXYGEN-CARRYING DEVICES IN OTHER ORGANISMS . . . 130
WHITE CORPUSCLES . . . 131
THE LIFE HISTORY OF WHITE CELLS . . . 134
Diseases of the Blood . . . 134
ANEMIA . . . 134
POLYCYTHEMIA . . . 135
LEUKEMIA . . . 135
Blood Platelets . . . 136
THE CLOTTING OF BLOOD . . . 136
Medico-Legal Tests for Blood . . . 138
Blood Types and Transfusions . . . 139

9. THE CIRCULATORY SYSTEM . . . 143

The Blood Vessels . . . 143
The Heart . . . 145
THE HEART BEAT . . . 147
THE HEART CYCLE . . . 149
ELECTRICAL CHANGES IN THE HEART . . . 151
ADAPTATION OF THE HEART BEAT TO BODY ACTIVITY . . . 153
Routes of the Blood around the Body . . . 153
FETAL CIRCULATION AND CHANGES AT BIRTH . . . 154
THE RATE OF THE FLOW OF BLOOD . . . 156
BLOOD PRESSURE . . . 160
THE ROLE OF BLOOD PRESSURE IN THE EXCHANGE OF MATERIALS IN THE CAPILLARIES . . . 162
Heart and Vessel Disorders . . . 164
The Lymph System . . . 165
THE FLOW OF LYMPH . . . 166
FUNCTIONS OF THE LYMPH SYSTEM . . . 166

Circulation in Other Organisms 167
CIRCULATION IN ANIMALS 167
CIRCULATION IN PLANTS 171

10. THE RESPIRATORY SYSTEM 173

DIRECT RESPIRATION 173
INDIRECT RESPIRATION 174
STRUCTURE OF THE HUMAN RESPIRATORY SYSTEM 174
THE MECHANICS OF BREATHING 178
THE QUANTITY OF AIR RESPIRED 179
COMPOSITION OF ALVEOLAR AIR 180
EXCHANGE OF GASES IN THE LUNGS 180
TRANSPORTATION OF OXYGEN BY THE BLOOD 181
TRANSPORTATION OF CARBON DIOXIDE BY THE BLOOD . . . 182
ASPHYXIA 183
ARTIFICIAL RESPIRATION 184
THE CONTROL OF BREATHING 184
THE EFFECTS OF TRAINING 186
THE EVOLUTION OF THE HUMAN LUNGS 186
RESPIRATORY DEVICES IN OTHER ANIMALS 188

11. THE DIGESTIVE SYSTEM 190

The Mouth Cavity 190
THE TONGUE 190
THE TEETH 193
THE SALIVARY GLANDS 193
Microscopic Anatomy of the Digestive Tract 194
The Pharynx 195
SWALLOWING 196
The Esophagus 196
The Stomach 197
VOMITING 198
The Small Intestine 198
INTESTINAL MOVEMENTS 199
The Liver 200
The Pancreas 201
The Absorption of Food 201
The Large Intestine and Rectum 203
Disorders of the Digestive Tract 205
The Chemistry of Digestion 205
SALIVA 206
GASTRIC JUICE 206
PANCREATIC JUICE 207
INTESTINAL JUICE 208
Methods of Stimulating the Digestive Glands 209
Comparison of Digestive Systems of Other Animals 211

12. METABOLISM AND NUTRITION 214

The Basal Metabolic Rate 215
ENERGY REQUIREMENTS 215
The Fuels 216
CARBOHYDRATES 216
FATS 216
PROTEINS 216
The Metabolism of Carbohydrates, Fats and Proteins 217
CARBOHYDRATE METABOLISM 218
FAT METABOLISM 219
PROTEIN METABOLISM 219
Other Components of the Diet 220
MINERALS 220
WATER 221
CONDIMENTS AND ROUGHAGE 221
VITAMINS 221
Diet 233

13. THE EXCRETORY SYSTEM 238

The Kidney and Its Ducts 239
THE FORMATION OF URINE 240
THE REGULATORY FUNCTION OF THE KIDNEY 243
SUBSTANCES PRESENT IN THE URINE 244
DISEASES OF THE KIDNEYS 244
Excretory Devices in Other Animals 245
Excretion in Plants 247

14. THE INTEGUMENTARY AND SKELETAL SYSTEMS . . . 248

The Skin 248
PARTS OF THE SKIN 249
OUTGROWTHS OF THE SKIN 250
The Skeleton 250
TYPES OF SKELETONS 251
PARTS OF THE SKELETON 252
THE JOINTS 253
TYPES OF LOCOMOTION 254
THE SKELETAL SYSTEM OF PLANTS 254

15. THE MUSCULAR SYSTEM 256

KINDS OF CONTRACTION 258
THE CHEMISTRY OF MUSCLE CONTRACTION 260
THE OXYGEN DEBT 262
FATIGUE 262
THE NATURE OF CONTRACTION 262

CARDIAC AND SMOOTH MUSCLE 263
THE MUSCLES OF LOWER ANIMALS 263

16. THE NERVOUS SYSTEM 265

NEURONS 265
THE NERVOUS IMPULSE 266
TRANSMISSION AT THE SYNAPSE 270
The Parts of the Nervous System 271
THE CENTRAL NERVOUS SYSTEM 271
BRAIN WAVES 277
SLEEP 277
INSANITY AND NEUROSES 278
THE PERIPHERAL NERVOUS SYSTEM 279
REFLEXES AND REFLEX ARCS 281
HABIT, MEMORY AND LEARNING 283
MOODS AND EMOTIONS 284
The Autonomic Nervous System 284
THE SYMPATHETIC SYSTEM 286
THE PARASYMPATHETIC SYSTEM 286
The Nervous Systems of Lower Animals 287
The Transmission of Impulses in Plants 288

17. THE SENSE ORGANS 290

THE STIMULUS-RECEIVING PROCESS 291
THE PERCEPTION OF SENSATIONS 291
LOCALIZATION AND INTENSITY OF STIMULI 292
THE TACTILE SENSES 292
KINESTHESIS 292
VISCERAL SENSITIVITY 293
THE CHEMICAL SENSES: TASTE AND SMELL 294
VISION 295
THE EAR 301

18. THE ENDOCRINE SYSTEM 308

The Thyroid Glands 310
The Parathyroid Glands 313
The Islet Cells of the Pancreas 315
The Adrenal Glands 317
THE ADRENAL MEDULLA 317
THE ADRENAL CORTEX 317
The Pituitary 318
THE POSTERIOR LOBE 319
THE ANTERIOR LOBE 320
The Testes 323
The Ovaries 325
THE ESTRUS CYCLE 326

THE MENSTRUAL CYCLE 326
The Placenta 328
Other Endocrine Glands 328
Interrelationships between the Endocrine Glands 329
Hormones in Lower Animals and Plants 329

Part IV. THE REPRODUCTIVE PROCESS

19. METHODS OF REPRODUCTION 333

Asexual Reproduction 334
Sexual Reproduction 336
The Life Cycle 338
THE LIFE CYCLE OF MOSSES 339
THE LIFE CYCLE OF THE FERN 341
THE LIFE CYCLE OF A SEED PLANT 341
Sexual Reproduction in Animals 344
HERMAPHRODITISM 344
PARTHENOGENESIS 344
TYPES OF FERTILIZATION 345

20. HUMAN REPRODUCTION 347

THE MALE REPRODUCTIVE ORGANS 347
THE FEMALE REPRODUCTIVE ORGANS 349
FERTILIZATION 351
IMPLANTATION 353
NUTRITION OF THE EMBRYO 353
THE EMBRYONIC MEMBRANES 353
THE PLACENTA 355
BIRTH 356
NUTRITION OF THE INFANT 358

21. EMBRYONIC DEVELOPMENT 361

TYPES OF EGGS 361
CLEAVAGE 362
BLASTULA FORMATION 362
GASTRULATION 362
CLEAVAGE AND GASTRULATION IN FROG AND CHICK EGGS . . 363
CLEAVAGE AND GASTRULATION IN THE HUMAN EGG 364
MESODERM FORMATION 365
THE NOTOCHORD 367
THE DEVELOPMENT OF THE NERVOUS SYSTEM 368
THE DEVELOPMENT OF BODY FORM 369
FORMATION OF THE HEART 373
DEVELOPMENT OF THE DIGESTIVE TRACT 375
THE DEVELOPMENT OF THE KIDNEY 375
THE CONTRIBUTIONS OF EACH GERM LAYER 377

CONTROL OF DEVELOPMENT 378
ORGANIZERS 378
TWINNING 379
THE CHANGES AT BIRTH 380

Part V. MICRO-ORGANISMS AND INFECTIOUS DISEASES

22. MICRO-ORGANISMS AND INFECTIOUS DISEASES 385

Bacteria 385
THE CARBON CYCLE 386
THE NITROGEN CYCLE 387
BACTERIA IN INDUSTRIAL PROCESSES 387
TYPES OF BACTERIA 387
REPRODUCTION OF BACTERIA 390
BACTERIAL METABOLISM 390
Other Micro-organisms 390
FILTERABLE VIRUSES 390
BACTERIOPHAGES 392
RICKETTSIA 393
FUNGI 394
PROTOZOA 395
Worms 395
Insects 395
Antibiotics 397
The Germ Theory of Disease 397
KOCH'S POSTULATES 398
How Micro-Organisms Cause Disease 399
Body Defenses against Disease 400
ACQUIRED IMMUNITY 401
NATURAL IMMUNITY 402
ALLERGY 403
The Spread of Micro-Organisms 404
Some Common Infectious Diseases 405
INFANTILE PARALYSIS 405
TYPHUS 405
SYPHILIS 405
ATHLETE'S FOOT 407
AMEBIC DYSENTERY 407
TAPEWORM INFECTIONS 408
TRICHINOSIS 409

Part VI. THE MECHANISM OF HEREDITY

23. THE PHYSICAL BASIS OF HEREDITY 413

CHROMOSOME STRUCTURE 415
CHROMOSOME NUMBER 415
MITOSIS 415

CONTROL OF MITOSIS . . . 419
MEIOSIS . . . 420
THE GENES . . . 426
ALLELES . . . 426
A MONOHYBRID CROSS . . . 427
PHENOTYPE AND GENOTYPE . . . 428
MENDEL'S FIRST LAW . . . 429
TEST CROSSES . . . 429
INCOMPLETE DOMINANCE . . . 430
DEDUCING GENOTYPES . . . 431

24. GENETICS . . . 434

Mendel's Second Law . . . 434
Interactions of Genes . . . 436
COMPLEMENTARY GENES . . . 436
SUPPLEMENTARY GENES . . . 437
MULTIPLE FACTORS . . . 439
MULTIPLE ALLELES . . . 441
LETHAL GENES . . . 441
The Genetic Determination of Sex . . . 443
SEX-LINKED CHARACTERISTICS . . . 444
SEX-INFLUENCED CHARACTERS . . . 444
Linkage and Crossing Over . . . 445
Penetrance and Expressivity . . . 447
Inbreeding and Outbreeding . . . 448
Biochemical Genetics . . . 450

25. INHERITANCE IN MAN . . . 453

Pedigrees . . . 453
The Inheritance of Physical Traits . . . 454
Inheritance of Mental Qualities . . . 457
INHERITANCE OF MENTAL DISORDERS . . . 457
INHERITANCE OF SPECIAL ABILITIES . . . 460
Eugenics . . . 460

Part VII. EVOLUTION AND ADAPTATION

26. PRINCIPLES AND THEORIES OF EVOLUTION . . . 467

ORGANIC EVOLUTION . . . 467
JEAN BAPTISTE DE LAMARCK . . . 469
BACKGROUND FOR THE ORIGIN OF SPECIES . . . 469
THE THEORY OF NATURAL SELECTION . . . 470
MODERN CHANGES IN THEORY OF NATURAL SELECTION . . . 471
PREADAPTATION . . . 473
MUTATION THEORY OF DE VRIES . . . 474

TYPES OF MUTATIONS 476
FREQUENCY OF MUTATIONS 476
CAUSES OF MUTATIONS 477
STRAIGHT-LINE EVOLUTION 477
THE ORIGIN OF SPECIES BY HYBRIDIZATION 479
PRINCIPLES OF EVOLUTION 480

27. THE FOSSIL EVIDENCE FOR EVOLUTION 482

Paleontology 482
The Geologic Time Table 486
The Geologic Eras 487
ARCHEOZOIC ERA 487
PROTEROZOIC ERA 487
PALEOZOIC ERA 487
THE MESOZOIC ERA (THE AGE OF REPTILES) 495
THE CENOZOIC ERA (THE AGE OF MAMMALS) 501

28. THE LIVING EVIDENCE FOR EVOLUTION 509

THE ANATOMIC EVIDENCE 509
THE EVIDENCE FROM COMPARATIVE PHYSIOLOGY AND BIOCHEMISTRY 510
THE EMBRYOLOGIC EVIDENCE 512
THE GENETIC EVIDENCE 515
EVIDENCE FROM THE GEOGRAPHIC DISTRIBUTION OF ORGANISMS 516

29. THE EVOLUTION OF MAN 520

Man and the Other Primates 520
Fossil Primates 527
Fossil Ape-Men 528
THE JAVA APE-MAN 530
PEKING MAN 530
PILTDOWN MAN 532
Fossil Members of the Genus Homo 532
HEIDELBERG MAN 533
NEANDERTHAL MAN 533
SOLO MAN 533
RHODESIAN MAN 534
MODERN MAN 534
Cultural Evolution 537
The Present Races of Man 540
THE WHITE RACE 541
THE NEGROID RACE 542
THE MONGOLOID RACE 543

30. THE OUTCOME OF EVOLUTION: ADAPTATION 547

ECOLOGY 547
BIOLOGICAL INTERACTIONS 547

STRUCTURAL AND PHYSIOLOGIC ADAPTATIONS 548
PHYSIOLOGIC ADAPTATIONS 550
COLOR ADAPTATIONS 550
TERRESTRIAL LIFE ZONES 552
MARINE LIFE ZONES 552

APPENDIX. SURVEY OF PLANT AND ANIMAL KINGDOMS . . 557

The Plant Kingdom 557
PHYLUM THALLOPHYTA 557
PHYLUM BRYOPHYTA 557
PHYLUM PTERIDOPHYTA 558
PHYLUM SPERMATOPHYTA 558
The Animal Kingdom 558
PHYLUM PROTOZOA 558
PHYLUM PORIFERA 559
PHYLUM COELENTERATA 559
PHYLUM CTENOPHORA 559
PHYLUM PLATYHELMINTHES 559
PHYLUM NEMERTEA 559
PHYLUM NEMATODA 559
PHYLUM ACANTHOCEPHALA 559
PHYLUM CHAETOGNATHA 559
PHYLUM NEMATOMORPHA 560
PHYLUM ROTIFERA 560
PHYLUM GASTROTRICHA 560
PHYLUM BRYOZOA 560
PHYLUM BRACHIOPODA 560
PHYLUM PHORONIDA 560
PHYLUM ANNELIDA 560
PHYLUM ONYCHOPHORA 560
PHYLUM ARTHROPODA 560
PHYLUM MOLLUSCA 561
PHYLUM ECHINODERMATA 561
PHYLUM CHORDATA 561

INDEX 565

CHAPTER 1

INTRODUCTION

WE SOMETIMES come into contact with a subject—memorize dates, figures, processes, and even come to certain conclusions about it—without really understanding it at all. History seems to be the most elusive field in this respect, and the sciences appear to be the most solid. Certainly when one says, "I'm studying Biology," he expects to be understood to say "I'm studying the science of life"—a seemingly meaningful statement without ambiguity.

But what exactly is "science" and what is "life?" Reflection on the latter word may arouse some doubts as to the unequivocal nature of biology, since no one knows the exact chemical composition of a single cell of the human body or of the smallest one-celled plant. Nor can anyone explain how living stuff came into existence. We have, then, only a rough idea of what life really is on even the simplest level, and we must admit that the professor of biology, like the student, is studying only certain manifestations or behavior which it is convenient to call life.

Accepting the limitation, let us glance at the range of living manifestations and see which are important for the biologist. At the present time, the earth is inhabited by a quarter of a million different kinds (species) of plants, and by a million kinds of animals. These figures indicate one of the most amazing and characteristic qualities of life—its diversity. When we compare such unlike forms as the microscopic plants living on the coral in the Indian Sea and the wolverines of Canada; the bacteria frozen in the Arctic ice and the Gila monsters of Mexico; the giant redwoods and the edelweiss of the Swiss Alps—to say nothing of the two billion human beings living in almost every environment the earth offers —we begin to realize how extravagantly, fantastically diverse life is.

Another striking fact emerging from such considerations is that it is almost impossible to talk about the forms of life without reference to their habitats. The animate world is inseparable from the inanimate one, and it is the whole globe, with all its oceans, mountains and deserts, as well as their incredible burden of struggling forms, which is involved in the word "life."

But even this is only half the story, as the diversity of life itself shows with its implication of time. We say it "takes time" for things to alter, but in reality, time *is* alteration, and the present forms of life with their interrelationships are living evidence of the alterations of the past. This is the temporal, the historical or evolutionary, aspect of the universe, as diversity and distribution comprise its spatial aspect.

In order to get an idea of the length of time—the number of events—involved in the evolution of life, one must remember that it was about a billion and a half years ago when life began to emerge from the slime of the nonliving; that the giant tree ferns (the source of our coal) existed

some 250,000,000 years ago; that the dinosaurs became extinct 60,000,000 years ago; and that man did not appear on the scene until about a million years ago. According to human notions, the world was old when man and his close relatives emerged from the previous apelike forms to begin their long, arduous battle to dominate the world. It is interesting to speculate about how the first men learned to communicate, to clothe and defend themselves, to hunt and fish. Coming to comparatively recent times, think what a complete reorganization of life, involving the migrations and readaptations of men, plants and animals, was caused by the four great glaciations, the last of which was only 20,000 years ago.

The date 5000 B.C. is important in human history since it is approximately the date of man's mastery of agriculture and animal husbandry. This revolutionary advance—generally considered the basis of civilization—affected the entire living world, for the new knowledge enabled man to change the shapes and distribution of plants and animals. Only 1000 years later, the Egyptians and Mesopotamians had developed advanced cultures, and by 3000 B.C. the Age of Metal was far advanced in Anatolia and the Aegean.

Within the historical period it is customary to use such events as the organization of the Greek city-states, the rise of the Roman Empire, the Middle Ages, the development of feudalism and the spread of the Renaissance as landmarks in studying history, but convenient as this practice is, there is a danger in it, for one tends to forget it was not the Western world alone or man as a species alone which were important, but the relationships between life forms in every part of the world.

Speculation about the framework just outlined may seem to carry us farther than ever from the special province of biology, since it is evident that the spatio-temporal universe embraces all fields of inquiry and should serve as a basis of investigations in esthetics or physics, as well as in history or biology. One thing it suggests, however, is that all the conceivable activities of the universe—and hence all the corresponding fields of knowledge—exist for us, not on a single plane, but on three different levels.

In a sense, the most basic of these is that concerned with the physical composition of the universe, which is the province of the modern sciences of physics and chemistry. Investigators on this level are trying to describe in terms of electrons, neutrons, atoms and molecules what lies behind the appearance of the familiar world, animate and inanimate.

Far removed from these problems, at least so it seems superficially, are such fields of investigation as those concerning consciousness, the relations of man to man, and other problems of the human predicament. History, psychology, sociology and political science illustrate this level of inquiry.

Between the two levels—that of the atom and that of the mind—lies a third, embracing the entire universe of sense perception, both animate and inanimate. On this level geology, astronomy and engineering are fields of knowledge dealing with the latter; biology, with all its subsciences, is concerned with the animate. Obviously, even the area restricted to biology is too broad to be completely investigated by one person, or treated thoroughly in a single textbook, so that most biologists

are specialists in a limited phase of the subject. The **zoologist** and **botanist** study types of organisms and their relationships within the animal and plant kingdoms, respectively; the **parasitologist** studies the forms of life which live on and at the expense of other forms; the **cytologist** investigates the composition and behavior of cells; and the **histologist** inquires into the properties of tissues. More familiar perhaps are the subsciences of **anatomy, physiology** and **embryology,** which deal with the structure, function and development of animals and plants, and are usually investigated in connection with a particular organism. The science of **genetics** is concerned with the transmission of the characteristics of one generation to succeeding ones, and is closely related to the study of **evolution,** which attempts to discover how new species arise, as well as how the present forms evolved from previous ones. And there is the classical study of plant and animal **taxonomy,** which has to do with giving names to the forms of life and dividing them into related groups. These fields of study are but a few of the many subdivisions of the science of biology.

We have at last arrived at a point where the special province of biology can be delineated. Instead of calling it simply the science of life, we can say that it is the study of that peculiar quality of life which is its aliveness. Biology is concerned with the forms which living things take, with their physical relationships, and with all those processes which set them off from the nonliving world. Thus, just as physics and chemistry are fundamental to biology, biology is in turn basic to the more "sophisticated" fields, and in order to grasp its essential significance, it must be studied in conjunction with other fields of activity. It is not enough simply to memorize large numbers of names and relationships (although of course, theories without facts are suspect, if not useless); one must see the subject as a part of the total panorama of existence. For example, the names and relationships of the human endocrine glands, as isolated pieces of information, are worthless; only when one discovers how they came into being, how they are related to comparable systems in other animals, and how they affect health and behavior, is the information either interesting or important. Perhaps biology has greatest value as a stepping stone to other investigations, and certainly some knowledge of it is indispensable in formulating a philosophy of life.

Fortunately, "science" is easier to define than "life," although its function is frequently misunderstood and is often both blamed and idolized without foundation. At the present time the word has taken on an almost magical significance for the nonscientist. People associate it with television and the atom bomb, forgetting that it is not science so much as the universe itself which is marvelous. Science is today just what it has always been—a tool, a method for discovering and organizing facts about the universe. Essentially, it is simply common sense carried to its logical conclusion and thus consists of three steps: observation, the formulation of theories, and the testing of those theories by controlled experiments.

There are, of course, many other sources of knowledge, or what various people believe to be knowledge: religious books such as the Bible and the Koran; novels and plays; books of magic; newspapers; tales of

mystic experiences; and bits of gossip passed on from person to person. In any of these sources of information there may be a great deal of truth, some small part of it, or none at all. We mention them only to contrast them with the method used for obtaining the information of biology —the scientific method.

Let us see how the method differs from, say that of superstition. Both superstition and the scientific method begin with observation. The primitive witch doctor, like the modern, civilized diagnostician, observes the phenomenon of disease and its two possible outcomes—recovery or death. He notices, too, that certain external conditions seem to modify it, that it progresses differently in different circumstances. One thing which tradition has taught him to notice is that after the performance of certain rituals, some of his patients get well. He therefore concludes that it is the practice of these rituals which cures them, and he continues to use the inherited formulas and to hand them down, in turn, to the next generation.

Meanwhile he has parted with the scientific method, not in suspecting a relationship between the rituals and the recovery, for the history of science abounds with seemingly much stranger relationships, but in accepting the "ritual" theory as true without testing it. Millions of civilized people fail in a similar way to follow the dictates of common sense when they refuse to walk under ladders, or to make appointments for Friday the 13th, or when they consult astrologists in order to avoid marrying on an "unpropitious" day. They part with science simply because, although disaster has undoubtedly overtaken people who walked under ladders, transacted business on Friday the 13th, and married on a "bad" astrological day, these acts have also been committed millions of times with impunity. In short, there is no *proof*—and little evidence—that a causal connection exists between such acts and the onslaught of misfortune.

The method of science is vividly and entertainingly presented in detective novels, such as the Sherlock Holmes stories. Holmes is a scientist *par excellence,* with his unfailing powers of observation enabling him to note the details of everything connected with his cases and his ability to conceive original theories based on relationships which poor Watson never grasps. It is here that imagination enters the scientific method, and it is the high development of this faculty which distinguishes the Einsteins from the conscientious plodders, just as it distinguishes man as a group from chimpanzees. (Chimpanzees and many other higher animals are capable of what is really logical thought, as exemplified by their problem solving. But because their imaginations are limited, they cannot "see around" and thereby solve complicated problems.) Finally, Holmes rounds out his other accomplishments by being patient and thorough in testing his theories, discarding those which experiments prove to be unfeasible. It is this same method carried on by hundreds of investigators all over the world and for many years which has yielded, and is still yielding, information about the biological world—such facts as how diseases are communicated and cured, and how characteristics are passed on from one generation to another.

Now that biology and its sources have been defined, we might pass on

to the subject itself, but one other item needs a bit of explanation. From the title of this book, which focuses attention on the human organism, one might suppose that man stands in the center of the living world with the other animals and the plants arranged around him. Actually, it is only in his own estimation that he forms a central pivot in the biological world. In point of numbers, size, strength, endurance and adaptability, man is inferior to many animals, and in adjustment to his environment—which, from the biological standpoint, might be considered a living creature's most valuable attribute—he often fails. Birds, ants and bees are much better adapted to living in the world than are human beings. One quality only does he excel in—intelligence—and, although it should not be underestimated, there is a question whether or not it is a "good" quality, again biologically speaking. The power to reason has the advantage of giving man control over his environment, thus making possible many pleasures and conveniences, but it is also the source of incalculable misery, in some cases sufficient to result in self-destruction. Quite justifiable, then, is the plan followed by many books of approaching the study of digestion, reproduction and disease from the standpoint of a crab or a hollyhock or some other animal or plant. But in a survey study of biology practical considerations as well as interest demand that man be in the center of the picture, since it is with the human stomach ache, the human gestation period, and the endurance of the human body that we must be primarily concerned.

PART I

BASIC STRUCTURES AND FUNCTIONS

CHAPTER 2

PHYSICOCHEMICAL BACKGROUND

MODERN BIOLOGY is different from what the ancients called "life science," and does not greatly resemble the biology of 400 years ago. Part of this difference is simply quantitative—the scope is broader today, and our knowledge is more detailed—but part of the difference stems from a shift in attitude, a new approach to the subject.

Biology had its inception, as did most sciences, in the questions aroused by the familiar objects of the everyday world. The first biologists were naturalists, interested primarily in seeing how many kinds of living things there were and in describing their differences and similarities. Such studies led in time to investigations of anatomy and physiology, and gradually a detailed record accumulated of the structures, functions and life habits of countless plants and animals. Then, as the picture of living organisms grew larger and clearer, biologists began to speculate about the development of organs and functions, their perviousness to disease, and what happens to them after the organism dies. In this way, descriptive embryology and pathology were initiated. These studies were essential, because in science, before any theorizing or experimentation can begin, someone must make thorough and accurate observations.

During the nineteenth century, biology began to alter and expand, reflecting the important new discoveries of physics and chemistry. The tools and knowledge contributed by investigators in the more basic fields enabled biologists to answer many questions which had puzzled naturalists for centuries. And in the last hundred years, more and more biologists have been drawn from the field of natural history into the level of inquiry represented by biophysics and biochemistry. This book is not primarily concerned with that level, but some knowledge of the fundamental, ultramicroscopic world is necessary for a real understanding of even the simplest physiological processes.

I. THE METRIC SYSTEM

In scientific discussions, measurements of any sort usually are not given in pounds, inches, ounces or any other units of the English system of measurement, because, for the purposes of science, the system proved cumbersome, due to the difficulty of changing from one unit to another. In France, at the time of the Revolution (1789) the English system was replaced by the metric system, which consists of units related in being multiples of ten. The basic unit, the **meter,** represents a certain fraction of the circumference of the earth and equals 39.37 inches. The units of weight and volume were derived from those of length. Thus the basic unit of volume, used for measuring small quantities, is the **cubic centimeter,** and the basic unit of weight, the **gram,** is the weight of 1

cubic centimeter of water under certain standard conditions. The **liter,** a measure of volume slightly larger than a quart, is the unit for greater quantities.

The superiority of the metric system over the English system is apparent: in order to change 0.58 liter to cubic centimeters, it is necessary only to move the decimal point three places to the right—580 cc. But to change 0.58 quart into ounces, one must multiply by 32 (since there are 32 ounces in a quart). Table 1 summarizes the units of the metrie

*Table 1. Some Common Units of the Metric System and Their English Equivalents**

Length

1 kilometer	(km.)	= 1000 meters	= 5/8 mile	
1 meter	(m.)	=	39.37	inches = 10 decimeters
1 decimeter	(dm.)	= 1/10 meter	= 4	inches = 10 centimeters
1 centimeter	(cm.)	= 1/100 meter	= 3/8	inch = 10 millimeters
1 millimeter	(mm.)	= 1/1000 meter	= 1/25	inch = 1000 microns
1 micron	(μ)	= 1/1000 millimeter	= 1/25,000	inch = 1000 millimicrons
1 millimicron	(mμ)	= 1/1000 micron	= 1/25,000,000	inch

Weight

1 kilogram	(kg.)	= 1000 grams	= 2.2 pounds	
1 gram	(gm.)	=	1/28 ounce	= 1000 milligrams
1 milligram	(mg.)	= 1/1000 gram	= 1/28,000 ounce	

Volume

1 liter (L.) =		1.06 quarts	= 1000 cubic centimeters
1 cubic centimeter (cc.)	= 1/1000 liter	= 1/30 fluid ounce	= 1000 cubic millimeters
1 cubic millimeter (cu. mm.)	= 1/1000 cc.	= 1/30,000 fluid ounce	

* The figures given as English equivalents are close approximations only.

system used in this book (there are many others) and gives the English equivalents, as well as the abbreviation for each term. Familiarity with the system and faeility in using it are helpful to the student of any science.

II. THE BASIC MATERIAL OF THE UNIVERSE

The universe is made up of two fundamental components—matter and energy—which in certain conditions are interconvertible. This is expressed by the famous Einstein equation: $E = mc^2$, where E = energy, m = mass, and c = the velocity of light, which is constant. In the familiar, everyday world, matter and energy appear separate, however, matter occupying space and having weight, and energy being the ability to produce a change or motion in matter—the ability to do work. But if all things, living and nonliving, are reducible to these components, the question immediately arises: what is responsible for the tremendous differences between the two kinds of things? The answer is the way in which the component parts are arranged. In living things the organization of the basic units is much more complex than it is in inanimate objects.

1. The Structure of Matter. Regardless of the form—gaseous, liquid or solid—that matter may assume, it is always composed of small units,

called **atoms.** In nature there are ninety-two different kinds of atoms, ranging from hydrogen, the smallest, to uranium, the largest. In addition to these naturally occurring atoms, five more, larger than uranium, have been created synthetically. All of them, natural and synthetic, are much smaller than the tiniest particle visible under the microscope. In fact, no one has ever seen an atom; their structure and functions have been inferred from tests made with many types of elaborate apparatus.

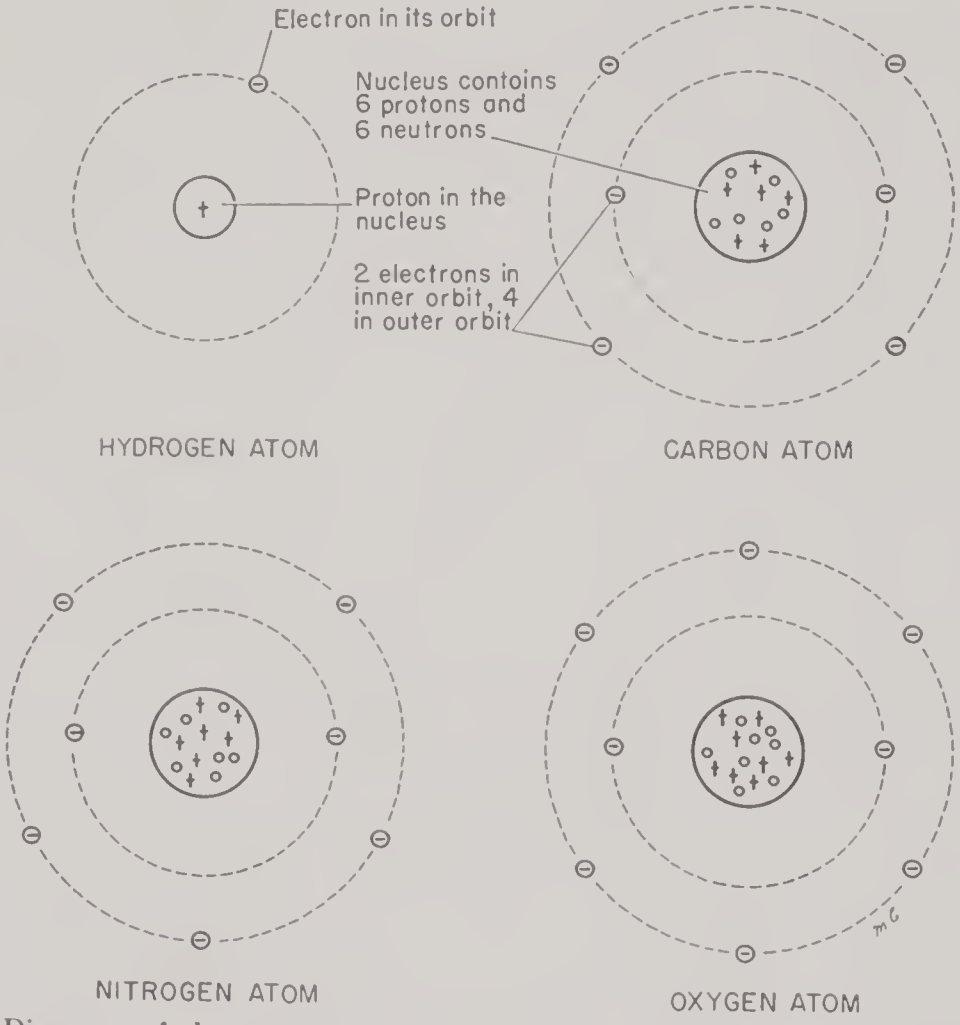

Electron in its orbit
Nucleus contoins 6 protons and 6 neutrons
Proton in the nucleus
2 electrons in inner orbit, 4 in outer orbit
HYDROGEN ATOM
CARBON ATOM
NITROGEN ATOM
OXYGEN ATOM

Fig. 1. Diagrams of the atomic structure of the four chief elements of the body. The nitrogen atom nucleus contains seven protons (+) and seven neutrons (O); its inner orbit has two electrons, and its outer orbit, five. The oxygen atom nucleus contains eight protons and eight neutrons, and there are two and six electrons, respectively, in its inner and outer orbits.

Once the atom was believed to be the ultimate, smallest unit of matter. Now physicists know that atoms are divisible into even smaller particles organized around a central core, as our solar system is organized around the sun. The exact number and kind of these particles and their arrangement in the atom are matters about which physicists are not in agreement. For our purposes we need consider only three types: **electrons,** which have a negative electric charge and an extremely small mass or weight; **protons,** which have a positive electric charge and are about 1800 times as heavy as electrons; and **neutrons,** which have no electrical charge, but have essentially the same mass as protons. The center of the atom, corresponding in position to the sun in our solar system, is the nucleus, containing protons, neutrons and perhaps elec-

trons as well; it comprises almost the total mass of the atom. Just as most of the solar system is empty space, so is the atom, with electrons revolving around the nucleus in definite paths or orbits. The various types of atoms have different numbers of electrons circling in their orbits, and different numbers of protons and neutrons in their nuclei, but in all atoms, the number of protons in the nucleus equals the number of electrons circling around it, so that a state of electrical neutrality is maintained. There are only a few kinds of particles besides electrons, protons and neutrons, perhaps no more than two or three. The different types of matter are produced by differences in the number and arrangement of these basic particles.

2. Types of Substances: *Elements.* Any substance composed of atoms which have the same number of electrons in their orbits is called an **element.** You are acquainted with the more common of these, such as gold, silver, iron and copper. The most common ones in living matter are hydrogen, oxygen, carbon and nitrogen (Fig. 1). Chemists have established a kind of shorthand for their own convenience by assigning symbols to the elements. The symbol usually is the initial letter of the element's name: O, oxygen; H, hydrogen; C, carbon; N, nitrogen. When several elements have the same initial letter, a second letter is added to the symbol: C, carbon; Cu, copper; Cl, chlorine.

During the last fifty years evidence has accumulated that most, if not all, elements are made up of two or more kinds of atoms, which differ in the number of neutrons in their nuclei. Thus there are sixteen kinds of lead, three kinds of hydrogen, five kinds of carbon, and so on. The different types of atoms of an element are known as **isotopes** (iso = equal; tope = place) because they occupy the same place in the periodic table of the elements (remember that the electrons in their orbits which are responsible for their chemical properties are the same).

With the development of the cyclotron and the nuclear reactor, or atomic pile, it became possible to make artificially many new isotopes, and when these became available, an entirely new type of biological research was opened up. For although the isotopes of a given element have the same *chemical* properties, they can be differentiated *physically.* Some of them are radioactive and can be detected with an instrument such as the Geiger counter, by the rays they emit. Others can be differentiated by the slight difference in the weight of the atoms caused by the extra neutron in the nucleus. By labeling or tagging a substance—some sugar molecules, for example—by substituting either radioactive carbon (C^{11} or C^{14}) or heavy carbon (C^{13}) for ordinary carbon (C^{12}), and then feeding or injecting it into an animal, one can trace the pathway the substance follows in the body as it is used and finally excreted. Many problems in physiology and biochemistry that could not be attacked in any other way can be solved by this method.

The chemical properties of elements depend chiefly on the number and arrangement of the electrons in the outer orbit and to a lesser degree on the electrons in the inner orbits, and on the number and kind of particles in the nuclei. The number of electrons in the outermost orbit varies from zero to eight in different atoms. If there are eight electrons in the outer orbit, the element is chemically inactive and will

not combine with other elements. When there are fewer than eight electrons, the atom tends to lose or gain some in order to achieve an outer orbit of eight. Since the number of protons (positively charged particles) in the nucleus remains the same, the loss or gain of electrons by an atom results in an electrically charged atom called an **ion.** Atoms with one, two or three electrons in the outer orbit tend to lose them to other atoms during chemical reactions and thus become positively charged because of the excess protons in the nucleus. Atoms with five, six or seven electrons in the outer orbit tend to gain electrons from other atoms and thus become negatively charged because of the excess electrons revolving around the nucleus. Atoms with four electrons in the outer orbit (such as carbon) may either lose or gain electrons. Both positively and negatively charged atoms are called ions. Because particles that have opposite electric charges attract each other, positive and negative ions tend to unite.

Compounds. A substance formed by the union of two or more different kinds of atoms or ions is called a **compound.** The smallest particle of a compound having the composition and properties of a larger part of the substance is called a **molecule.** A **pure compound** is always made of two or more elements united in a definite ratio. Water, for example, always contains two atoms of hydrogen for every atom of oxygen; hence the chemical formula, H_2O. In contrast, a **mixture** is made of two or more kinds of atoms or molecules which may be combined in different proportions. Thus water and alcohol may be mixed in all proportions, and air is a mixture of varying amounts of oxygen and nitrogen, plus small quantities of carbon dioxide, argon and other gases. It follows that a pure compound will exhibit certain fixed chemical and physical properties, whereas a mixture will have properties that vary with the relative abundance of its constituents. A molecule of glucose (a simple sugar) is composd of six carbon atoms, twelve hydrogen atoms and six oxygen atoms, and therefore has the formula $C_6H_{12}O_6$. Any larger portion of glucose—a gram, for instance—will also contain carbon, hydrogen and oxygen in the same proportions. If it were possible to divide a gram of glucose in half, then divide the half in half, then the quarters in half, and so on, eventually the glucose would be subdivided into its constituent molecules, each of which would have the same composition and properties as the original gram. However, if a glucose molecule were divided, the parts no longer would be sugar, but would be carbon, hydrogen and oxygen atoms, and would have quite different properties.

The molecules of a few substances are composed of only one kind of atom—oxygen and nitrogen, for example, exist in the atmosphere as O_2 and N_2, each molecule being made of two of the same kind of atom. The molecules of some other substances contain several kinds of atoms: a molecule of table salt, or sodium chloride, is made of one atom of sodium (Na, from its Latin name, *natrium*) and one of chlorine (Cl). A glucose molecule is slightly more complex, being composed of three kinds of atoms; and some molecules, such as those of proteins, are enormously complex structures made of thousands of atoms.

Acids. Some compounds release hydrogen ions when dissolved in water, and are called **acids.** Acids have a sour taste and the ability to

change the color of blue litmus paper to red. (Litmus is an indicator, a substance which will change color in the presence of an acid or an alkali.) Two common examples of acids are vinegar, which contains acetic acid, and sour milk, which contains lactic acid.

Alkalis. **Alkalis** are compounds which release hydroxyl ions when dissolved in water. A hydroxyl ion is made of an oxygen atom and a hydrogen atom bound together (expressed as OH), and has a negative electric charge. Alkalis turn red litmus paper blue. Typical alkalis are sodium hydroxide (NaOH) and household ammonia or ammonium hydroxide (NH_4OH).

In stating the amount of acidity or alkalinity of a fluid, the concept of *p*H is used. Thus, a *p*H of 7 indicates a substance that is neutral, neither acid nor alkaline. A *p*H less than 7 indicates an acid, and one over 7 indicates an alkali (the scale extends to 14). Because the scale is logarithmic, a substance with a *p*H of 5 is ten times as acid as one with a *p*H of 6; a substance with a *p*H of 10 is 100 times as alkaline as one with a *p*H of 8; and so on.

Salts. When an acid and an alkali are mixed, the hydrogen ion of the acid unites with the hydroxyl ion of the alkali to form water, and the rest of the acid unites with the rest of the alkali to form a **salt.** Thus hydrochloric acid (HCl) mixed with sodium hydroxide (NaOH) produces water (H_2O) and common table salt (NaCl), which is just one of the many compounds known as salts. Salts may be defined briefly as compounds in which the hydrogen atom of an acid is replaced by some metal. They may be produced in other ways than by mixing an acid and an alkali—by the action of an acid on a metal, for example.

Salts, acids and alkalis, when dissolved in water, separate into their constituent ions, and these charged particles can conduct an electric current. Such substances are called **electrolytes.** Other substances such as sugars and alcohols, which do not separate into ions when dissolved, and therefore do not conduct an electric current, are called **nonelectrolytes.**

3. Chemical Reactions. The mixing of hydrochloric acid and sodium hydroxide is an example of a **chemical reaction.** Chemical reactions are expressed in symbols with a plus sign connecting the substances which interact or result, and an arrow indicating the direction in which the chemical reaction proceeds.

$$HCl + NaOH \longrightarrow NaCl + H_2O$$

Notice that there is the same number of each kind of atom on each side of the arrow, since atoms are neither destroyed nor created in a chemical reaction, but simply change partners. This is an expression of one of the basic tenets of physics, the Law of the Conservation of Matter. The energy relations of the several chemicals involved, their relative concentrations and their solubility are some of the factors involved. Under certain conditions some chemical reactions are reversible: they may go from right to left or in the opposite direction, depending upon the factors just mentioned. Reversible reactions are indicated by a double arrow: $\rightleftharpoons$.

The rate at which chemical reactions occur is determined by a number

of factors, one of which is temperature. Each increase of 10° C. approximately doubles the rate of reaction. This is true of biological processes as well as of reactions in a test tube, indicating that the chemical reactions of living things are not fundamentally different from those of nonliving ones.

4. Energy. Energy has been defined as the ability to do work or produce a change in matter; it may take the form of heat, light, electricity or motion. Physicists recognize two kinds of energy: **potential,** the ability to do work, owing to the position of a particle; and **kinetic,** the energy of motion. A rock at the top of a hill has potential energy; as it rolls down hill, the potential energy becomes kinetic energy. The potential energy of water at the top of a dam may be transformed into kinetic energy if it is harnessed to a water wheel. Energy is stored in food as potential energy, due to the position of the atoms in the food molecules. Then, inside the body, chemical reactions occur which change this potential energy into heat, motion or some other kind of kinetic energy. Living organisms are constantly transforming potential energy into kinetic energy, or vice versa. Under experimental conditions the amount of energy entering and leaving any given system may be measured and compared. It is always found that energy is neither created nor destroyed, but only transformed from one form to another. This is an expression of another fundamental law of physics, the Law of the Conservation of Energy. Living things as well as nonliving systems obey this law.

5. Types of Mixtures: *Solutions.* When a substance is mixed with water or some other liquid, one of three types of mixtures results. In one type, called a **true solution,** the ions or molecules of the dissolved substance (the solute) are dispersed among those of the dissolving liquid (the solvent). These dispersed particles are extremely tiny, either atoms or small molecules. True solutions are transparent and have a higher boiling point and a lower freezing point than pure water. Most acids, bases, salts and some nonelectrolytes, such as sugar, form true solutions when added to water.

Suspensions. Other substances, such as clay, break up into relatively large particles and form a **suspension.** The dispersed particles in a suspension are made of aggregates of large numbers of molecules, which settle out if the suspension is allowed to stand. Thus the particles of clay in muddy water will fall to the bottom if the water is not stirred constantly. Suspensions are not transparent and have the same boiling and freezing points as pure water.

Colloids. If the dispersed particles are intermediate in size (between 0.1 and 0.001 micron in diameter), too small to settle to the bottom, but too large to form a true solution, the mixture is known as a **colloid,** or colloidal solution. Many common substances are colloids—mayonnaise, cream, butter, jello, glue, fog and soap are just a few. There are several types of colloids: a solid in a liquid, such as glue; a solid in a gas, such as smoke; and a liquid in a gas, such as fog. A type of colloid in which a liquid is suspended in a liquid—such as cream, which consists of droplets of oil dispersed in water—is called an **emulsion.** All these are colloids because of the size of the dispersed particles. Colloids are

transparent or translucent, have about the same boiling and freezing points as pure water, and are stable—that is, they do not separate into their constituent parts on standing.

Colloids are unique in their ability to change from a liquid condition, known as a **sol,** to a solid or semisolid condition, known as a **gel.** When the contents of a package of gelatin are dissolved in hot water, the particles of gelatin are dispersed throughout the water and a liquid colloidal solution, a sol, results. As the gelatin cools, the gelatin particles become the continuous phase, the water particles become dispersed discontinuously throughout the gelatin, and a semisolid gel, the "jello" results. When reheated, the gel becomes a sol again. It is not always necessary to change the temperature in order to change a sol to a gel—when cream is beaten it changes from a liquid, sol condition to the semisolid, gel condition of whipped cream. Not all colloids are reversible; some are destroyed by changes in acidity, alkalinity or temperature. The particles coagulate, aggregate into larger particles (thus becoming a suspension) and finally settle out. Egg white is a colloid which, when heated, coagulates. The particles of a colloid may have either a positive or a negative charge. Usually, the particles of a given colloidal system have the same charge, so that the particles tend to repel each other and so remain dispersed and uncoagulated.

Many of the properties of colloids depend upon the enormous amount of surface area between the dissolved particles and the dissolving medium. The surface area obviously increases manyfold as a substance is divided into finer particles. A cube 1 cm. on each edge has a surface area of 6 square cm. When this is cut into eight cubes, each 0.5 cm. on an edge, each cube has a surface of 1.5 square cm., or a total area of 12 square cm. for the eight cubes. If the cube were divided into particles 100 microns on an edge, the total surface area would be 600 square cm.; and if the cube were divided into particles of colloidal size, say 0.01 micron on an edge, the total surface area would be 6,000,000 square cm. Since many chemical reactions can occur only at a surface, a colloidal system is a much better medium for rapid and frequent reactions than is any other type of mixture.

6. The Motion of Molecules. The molecules which make up all kinds of substances are constantly in motion. At first thought this seems difficult to believe, for many of the world's objects seem undeniably solid and stationary. But the fact is that the molecules which make up the bricks of a house or the granite of a mountain are constantly vibrating back and forth within an extremely small space. The chief difference between the three states of matter—solid, liquid and gas—is simply the freedom of movement of the molecules involved. The molecules of a solid are restricted to vibration; the molecules of a liquid move about with considerable freedom; and the movements of molecules in the gaseous state are restricted only by external barriers. This movement is caused by the inherent heat energy of the molecules.

It is characteristic of molecules in liquids and gases to diffuse, or move, in all directions until they are spread evenly throughout the available space. **Diffusion** may be defined as the movement of molecules from a region of high concentration to one of lower concentration,

because of their inherent heat energy. The physical process of diffusion is important in many biological phenomena, and examples are familiar to everyone. If a room is tightly closed to eliminate air currents, and perfume is released in one corner of the room, the molecules of perfume will spread out from the original corner where the high concentration exists, to all parts of the room (regions of lower concentration). Or if a lump of sugar is dropped in a beaker of water, the sugar dissolves and

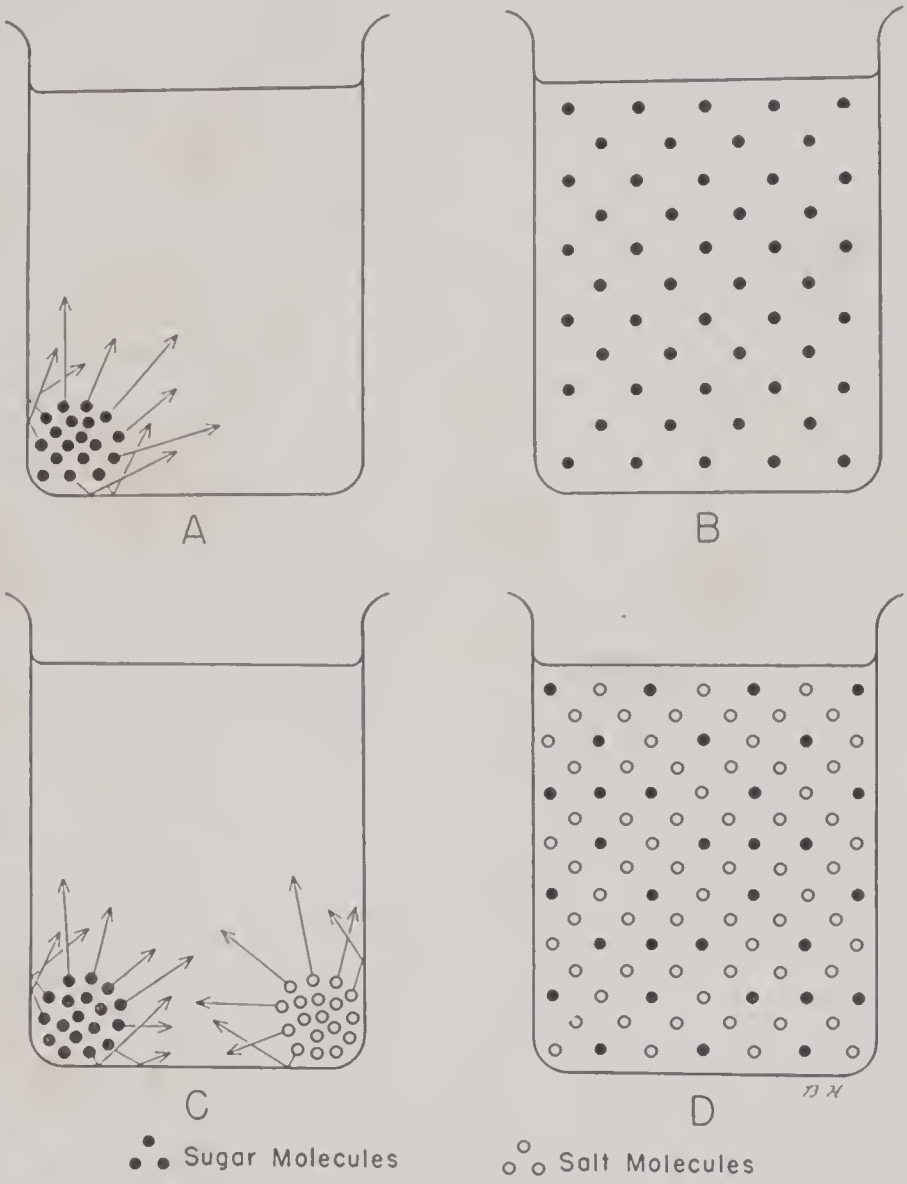


Fig. 2. Diffusion. *A*, When a lump of sugar is dropped in a beaker of water, its molecules dissolve and begin to diffuse. *B*, As a result of diffusion, the sugar molecules are dispersed evenly throughout the water in the beaker. *C*, When lumps of both sugar and salt are placed in a beaker of water, each type of molecule diffuses independently of the other. *D*, as a result, both sugar and salt molecules are spread evenly throughout the beaker of water.

the individual sugar molecules diffuse from the original position in the beaker (Fig. 2, *A*) and come to be spread equally throughout the liquid (Fig. 2, *B*). The individual molecules move in a straight line until they bump into something—another molecule or the side of the container; then they rebound and move in another direction. That the sugar molecules have diffused from their original corner to all parts of the beaker could be proved by withdrawing a few drops of liquid from the beaker with a medicine dropper and tasting them. The molecules continue to move after they have spread throughout the beaker; however,

as fast as some molecules move from left to right, others move from right to left, so that an equilibrium is maintained.

Any number of substances will diffuse independently of each other. If a lump of salt is dropped into another corner of the same beaker where the sugar has been deposited (Fig. 2, *C*), its molecules will spread out in all directions, unaffected by the sugar molecules, so that each drop of water in the beaker will have some salt and some sugar molecules (Fig. 2, *D*). Diffusion occurs more rapidly in gases than in liquids, but will occur even in solids though extremely slowly.

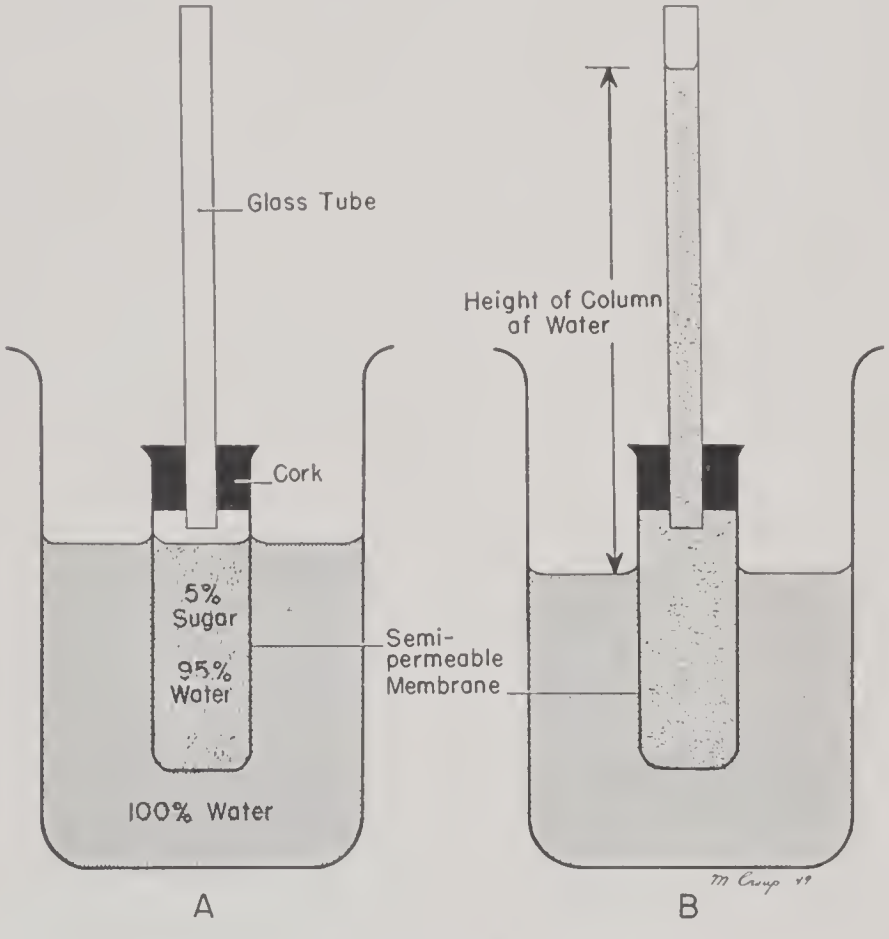


Fig. 3. Diagram illustrating osmosis. *A*, When a 5 per cent sugar solution is placed in a sac made of a semipermeable membrane, such as collodion, and suspended in water, the water molecules diffuse into the sac, causing the column of water in the glass tube to rise. *B*, When equilibrium is reached, the pressure of the column of water in the tube just equals, and is a measure of, the osmotic pressure of the sugar solution.

7. Membranes. If a membrane is introduced into a diffusing system, some additional factors come into play. Whether or not a membrane will permit a certain substance to pass through it depends on its structure. A membrane is said to be **permeable** if it will permit any substance to pass through, **impermeable** if it will permit no substance to pass, and **semipermeable** if it will allow some but not all substances to diffuse through. Permeability is a property of the membrane, not of the diffusing substance. Only semipermeable membranes are important biologically, since they surround the living substance of all animals and plants.

The diffusion of a dissolved substance through a semipermeable membrane is called **dialysis.** If we stretch a semipermeable membrane made

of collodion, cellophane or parchment across a beaker, and drop a lump of sugar on one side of it, the sugar molecules will dialyze (if the membrane is permeable to sugar) and come to be equally distributed throughout the beaker. A semipermeable membrane has extremely tiny pores through which the molecules pass. The size of the pores limits the size of the molecules which may dialyze, so that in general large molecules cannot dialyze, but smaller ones can. Factors other than size, such as the electric charge, if any, carried by the diffusing particles, may also be important in determining whether dialysis will take place.

If a membrane permeable to water but not to sugar molecules is made in the form of a bag, filled with 5 per cent sugar solution, tightly stoppered with a cork through which a glass tube runs, and then put in a beaker of water, so that the levels of the water and sugar solution are identical (Fig. 3, *A*), a different type of diffusion may be observed. The sugar molecules are unable to penetrate the membrane, and so remain inside the bag. The water molecules, however, diffuse through the membrane into the sugar solution. Since the liquid inside the membrane is 5 per cent sugar, it is only 95 per cent water. The liquid outside the membrane is 100 per cent water. Therefore the water molecules move from a region of higher concentration (100 per cent, outside the membrane), to a region of lower concentration (95 per cent, inside the bag). This diffusion of water or solvent molecules through a membrane is called **osmosis.** As osmosis occurs, the water rises in the glass tube (Fig. 3, *B*). If an amount of water passes through the membrane equal to the amount of water originally inside the bag, the sugar solution will be diluted to 2.5 per cent sugar and 97.5 per cent water, but the concentration of water on the outside will still be higher than that on the inside and osmosis will continue. Eventually the water in the glass tube will rise to a height such that the weight of the water in the glass tube will exert a pressure just equal to the tendency of the water to pass through the membrane. Then no additional water will pass through, or rather, osmosis will occur in both directions through the semipermeable membrane with equal speed. The pressure of the column of water just equals, and is therefore a measure of, the **osmotic pressure** of the sugar solution. This osmotic pressure is brought about by the tendency of the water molecules to pass through the semipermeable membrane and equalize the concentration of water molecules on the two sides of the membrane. A more concentrated sugar solution would "draw" water to a higher level in the tube and thus have a greater osmotic pressure. A 10 per cent sugar solution would cause water to rise approximately twice as high in the tube as a 5 per cent solution.

The phenomena of dialysis, osmosis and osmotic pressure are extremely important in biological processes. Dialysis and osmosis are simply two special forms of diffusion. Diffusion is the general term for the movement of molecules from a region of high concentration to one of lower concentration, owing to their inherent heat energy. Dialysis is the diffusion of dissolved molecules through a semipermeable membrane. Osmosis is the diffusion of solvent molecules through a semipermeable membrane. In living things the solvent material is almost always water.

Dissolved in the fluid of every living cell are various materials—salts.

sugars and so on—which give the fluid a certain osmotic pressure. When a cell is placed in a fluid with the same osmotic pressure as its own, water does not enter or leave the cell (it neither shrinks nor swells), and the fluid is said to be **isotonic** to it. Normally, the blood and all the body fluids are isotonic; that is, they contain the same amount of dissolved material as the body cells. If a fluid contains more dissolved substances than a cell, water tends to pass out of the cell, causing it to shrink. Such a fluid is said to be **hypertonic** to the cell. Finally, if a fluid contains less dissolved material than a cell, water tends to enter the cell, causing it to swell. In this case the fluid is said to be **hypotonic** to the cell. A solution of 0.9 per cent sodium chloride (physiological saline) is isotonic to human cells. Red blood cells placed in a solution of 0.6 per cent sodium chloride swell and burst, whereas in a 1.3 per cent solution they shrink.

QUESTIONS

1. Differentiate between an element and a compound.
2. What is the relationship between atoms and molecules?
3. What is the meaning of the symbol *p*H? Why is it important?
4. What is the difference between acids, alkalis and salts?
5. Why does the mixing of alcohol and water not constitute a chemical reaction?
6. In what ways do gases, liquids and solids differ?
7. Why do colloids afford a particularly good base for chemical reactions?
8. Differentiate between diffusion, dialysis and osmosis.
9. What is the exact meaning of the following terms: atom, isotope, ion? Could a single particle of matter be all three simultaneously?

SUPPLEMENTARY READINGS

Conant, J. B.: *On Understanding Science.* New Haven, Yale University Press, 1947.
An interesting short history of science and exposition of the place of science in society.

Sedgwick, W. T., Tyler, H. W., and Bigelow, R. P.: *A Short History of Science.* New York, The Macmillan Company, 1939.
A well-written account of the historical development of the sciences.

Solomon, A. K.: *Why Smash Atoms?* Cambridge, Harvard University Press, 1943.
An entertaining introduction to the subject of atoms, neutrons and isotopes.

CHAPTER 3

PROTOPLASM

THE BODIES of human beings, as well as those of other animals and of plants, are composed of a substance called **protoplasm.** This basic, living material is not homogeneous, but varies among organisms and among the different organs of a single animal or plant. From time to time, even a single organ may change in composition. All the many kinds of protoplasm share certain physical and chemical characteristics, however, and whatever the secret of life may be, it is well hidden in this exceedingly complex substance.

I. PHYSICAL CHARACTERISTICS OF PROTOPLASM

We cannot see protoplasm on the surface of the human body because the living stuff is covered with a dead, protective layer of skin. In order to see how the fundamental matter of life looks, it is necessary to examine some simple animal or plant, like the ameba or slime mold, in which the protoplasm is naked and hence visible under the microscope. The protoplasm of such an organism seems colorless or perhaps faintly yellowish or greenish. Structurally it varies, sometimes appearing fibrillar or granular, and again exhibiting a netlike or honeycomb pattern. Invariably, it has a thick, viscid, syrupy consistency and would feel slimy to the touch.

Most of the peculiar qualities of protoplasm depend upon the fact that it is a colloidal system, a mixture of one substance, in the form of tiny particles, with another substance. In this case, the protein molecules, being too large to form a true solution with water, and too small to settle out, are dispersed throughout the medium and form a colloidal suspension.

Protoplasm is constantly and rapidly changing from the sol to the gel state and back, and the inherent capacity to do this is absolutely essential for it to remain alive. If the temperature is raised beyond a certain point, or if certain chemicals are applied to it, protoplasm is irreversibly changed into a gel or a sol and dies.

II. CHEMICAL COMPOSITION OF PROTOPLASM

1. Elements. The unique property of protoplasm, its aliveness, does not depend upon the presence of some rare or unique element. Four elements, carbon, oxygen, hydrogen and nitrogen, make up about 96 per cent of the material of the human body. Another four, calcium, phosphorus, potassium and sulfur, constitute 3 per cent of the body weight. Minute amounts of iodine, iron, sodium, chlorine, magnesium, copper and perhaps other elements complete the list. All these elements, and especially the first four, are abundant in the atmosphere, the earth's

crust and the sea. Life depends upon the complexity of the interrelationships of these common, abundant elements.

2. Compounds: *Water.* The elements just mentioned usually occur in protoplasm as chemical compounds, rather than singly as elements. A large part of protoplasm (about two-thirds of the body by weight) is simply water (H_2O). In man the percentage of water in protoplasm varies in different tissues, from about 20 per cent in bone to 85 per cent in brain cells. In jellyfish as much as 95 per cent of the protoplasm may be water. The water is extremely important as the dispersing phase of the colloidal system, for the chemicals involved in the reactions basic to life require a water medium in order to react. All the waste products of living, as well as these chemicals, are dissolved in it. Furthermore, since water has a vast capacity for absorbing heat without greatly altering its own temperature, it is important in protecting protoplasm against sudden thermal changes. It has also the property of absorbing a great deal of heat as it changes from a liquid to a gas, thus enabling the body to dissipate excess heat by the evaporation of sweat. The characteristic high heat conductivity of water makes it possible for heat to be distributed evenly throughout the body tissues. Finally, water is indispensable as a lubricant, being present in body fluids wherever one organ rubs against another, and in the joints where one bone moves on another.

Mineral Salts. Protoplasm contains a variety of mineral salts, of which sodium, potassium, calcium and magnesium are the chief positively charged ions, and chlorine, carbonate, phosphate and sulfate are the most common negatively charged ions. A complete analysis of the body fluids shows that both in the kinds of salts present and in their relative concentration, they remarkably resemble sea water. When protoplasm first originated (which most biologists believe to have occurred in the sea) it probably incorporated the salts of its environment, thereby becoming adapted to living in the presence of these salts. Then, when larger marine organisms evolved from the original ones, their body fluids were obtained from the surrounding sea water. Undoubtedly the process was repeated when the land forms evolved from the marine organisms, so that the body fluids of present-day land animals, including man, have essentially the same composition as sea water. Dr. Macallum of Toronto has suggested that the concentration of salts in the body fluids of mammals today (about 0.9 per cent by weight) reflects the concentration of salts in the sea during the Cambrian period when the ancestors of the land animals left the sea. The difference between this and the concentration of salts in the sea today, about 1.035 per cent by weight, may represent the increase in the salt content of the sea brought about by the constant leaching of the land over the approximately 550,000,000 intervening years.

Although the salts are present in low concentration in the body fluids, they have a marked influence on cell function. The concentration of the various salts is extremely constant under normal conditions, and any great deviation from the normal causes marked effects, even death. Heart muscle can contract normally only in the presence of the proper balance of sodium, potassium and calcium ions. If a frog heart is removed and placed in a pure sodium chloride solution, it soon stops

beating, in a relaxed condition. If placed in a solution of potassium chloride or a mixture of sodium and calcium chloride, it will stop in the contracted condition. It will continue to beat, however, if placed in a solution containing the proper balance of these three salts. A decrease in the concentration of calcium ions in the blood of mammals results in convulsions and death.

In addition to these specific effects of particular salts on protoplasm, the mineral salts are important in maintaining the osmotic balance between protoplasm and its environment.

3. Organic Compounds. Chemical compounds which contain carbon (with the exception of the carbonates) are known as organic compounds. Because of the structure of the carbon atom (see Fig. 1) and the fact that it can either gain or lose four electrons from its outer orbit, carbon can form a much greater variety of compounds than can any other element. In fact, one of the largest branches of chemistry, organic chemistry, deals only with these compounds and their reactions.

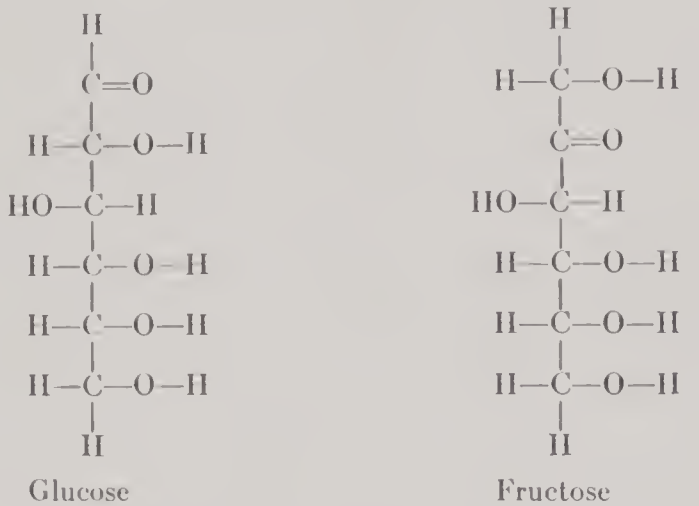


Fig. 4. Structural formulas of two simple sugars.

Though it was once believed that organic compounds could be produced only by living cells, in 1828 the German chemist Wöhler succeeded in artificially producing urea from the inorganic substance ammonium carbonate. Urea is an organic compound found as a waste product in the urine of vertebrates. Since that time an enormous number of organic compounds have been synthesized, and it is recognized that there is no essential difference between organic and inorganic compounds. Organic compounds are fundamental to the chemistry of protoplasm. The three main groups found in protoplasm are **carbohydrates, fats** and **proteins.**

Carbohydrates. Carbohydrates are compounds containing only carbon, hydrogen and oxygen. These are present in the ratio of 1C:2H:1O. Sugars, starches and cellulose are examples of carbohydrates.

The simplest carbohydrates found in protoplasm are the **simple sugars,** which have the formula $C_6H_{12}O_6$. There are several of these simple sugars, all generally similar, but differing in minor chemical properties, because of variations in the arrangements of the atoms within the molecule. Similar differences caused by variations in the internal structure of the molecule are frequently found in organic chemistry. **Glucose,**

(also called dextrose) and **fructose** are two simple sugars with the formula $C_6H_{12}O_6$, but with certain differences in their chemical properties. Chemists show these internal structural differences by drawing **structural formulas** of such compounds (Fig. 4). Hydrogen has one bond to connect to other atoms; oxygen, two; and carbon, four (see Fig. 1 for the structure of these atoms and the number of electrons they may gain or lose to form compounds).

Glucose is the only simple sugar found in any quantity in the body. The liver changes all the carbohydrates which are digested into glucose, since that is the only sugar protoplasm uses as fuel. Glucose is an absolutely indispensable component of blood. Normally it is present in the blood and tissues of mammals in a concentration of about 0.1 per cent by weight. No particular harm results from a simple increase in the amount of glucose in the body, but a reduced concentration increases the irritability of certain brain cells, so that they respond to very slight stimuli. As a result of impulses from these cells to the muscles, muscular twitches, convulsions, unconsciousness and death may ensue. It is not clear why these brain cells depend on a particular concentration of glucose for normal functioning, but there is an extremely complex mechanism, involving the nervous system, liver, pancreas and adrenal glands, which maintains the proper concentration.

A second group of carbohydrates found in protoplasm is the **double sugars,** which have the formula $C_{12}H_{22}O_{11}$. As their name implies, they are made of two simple sugars joined together by the removal of a molecule of water:

$$2C_6H_{12}O_6 \longrightarrow C_{12}H_{22}O_{11} + H_2O$$

Both cane and beet table sugars are **sucrose,** a combination of one molcule of glucose with one of fructose. Many other double sugars are

Table 2. Relative Sweetness of Some of the Common Sugars

Sugar	Relative Sweetness (Sucrose 100)
Lactose	16.0
Galactose	32.1
Maltose	32.5
Glucose	74.3
Sucrose	100.0
Fructose	173.3

known, all with the formula $C_{12}H_{22}O_{11}$, but differing in the arrangement of their constituent atoms and hence in some of their chemical and physical properties. **Maltose** or malt sugar is composed of two molecules of glucose; **lactose** or milk sugar, found in the milk of all mammals, is made of one molecule of glucose and one of **galactose,** a third kind of simple sugar. These sugars differ markedly in the degree of their sweetness. Fructose is the sweetest of the common sugars. Lactose, the least sweet, is less than one-tenth as sweet as fructose. Sucrose is intermediate (see Table 2).

The carbohydrates with the largest molcules are the **compound sugars,** starches and cellulose, composed of great numbers of simple

sugars joined together. Since the exact number of sugar molecules joined to make starch is unknown, the formula for starch may be written $(C_6H_{10}O_5)x$, where x stands for the unknown, large number of simple sugars which combine to make the starch molecule. Starches vary in the number and kind of sugar molecules they contain, and are common constituents of both plant and animal protoplasm. Animal starch, which is slightly different from plant starch, is called **glycogen**. Carbohydrates are stored in plants as starches and in animals as glycogen, because these molecules are too large to dialyze through the semipermeable membrane around the cell. Readily convertible into glucose, glycogen serves as an excellent storage mechanism. Most of it remains in the liver, although some stays in the muscles, and in these places it is converted as needed into glucose and carried by the blood to other parts of the body. Glucose could not be stored in a cell as such because it

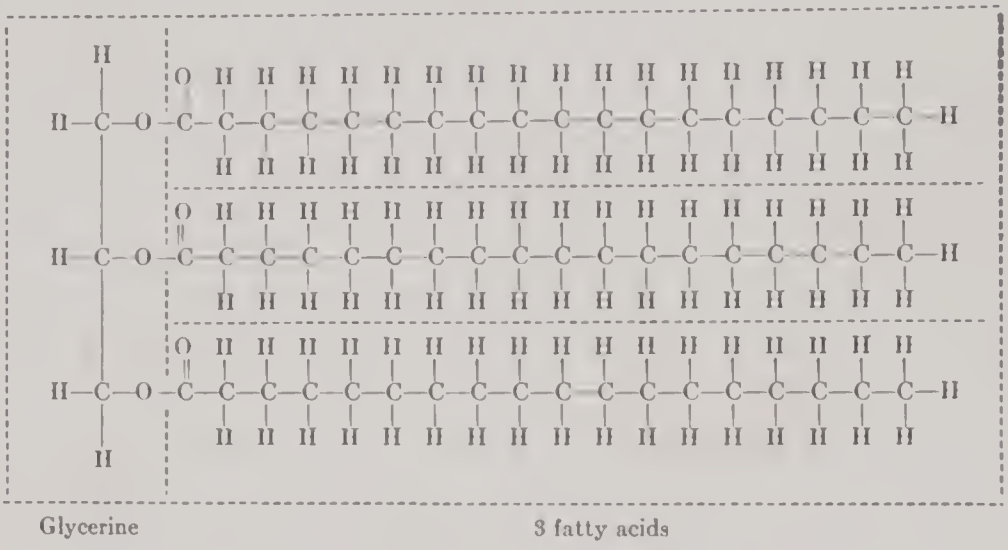


Fig. 5. Structural formula of a molecule of tristearin, a fat found in beef tallow.

would tend to diffuse out. Most plant cells have a strong supporting outer wall of *cellulose*, an insoluble compound sugar resembling starch in that it is made of many glucose molecules. Chemical compounds of cellulose are extremely important commercially; explosives, rayon, celluloid, certain plastics, photographic film and varnishes are a few of the commercial products.

The chief role of carbohydrates in protoplasm is that of a readily available fuel which supplies heat and energy. Glucose is oxidized or "burned," yielding water, carbon dioxide and energy:

$$C_6H_{12}O_6 + 6O_2 \longrightarrow 6H_2O + 6CO_2 + \text{energy}$$

To a slight extent, carbohydrates may enter into the structure of protoplasm and thus serve as building material as well as fuel.

Fats. True fats are also composed of carbon, hydrogen and oxygen, but have much less oxygen in proportion to the carbon and hydrogen than carbohydrates. A fat common in beef tallow is tristearin, $C_{57}H_{110}O_6$ (see Fig. 5). Each molecule of fat is composed of one molecule of glycerol and three molecules of some fatty acid. (Tristearin has three molecules of stearic acid, $C_{18}H_{36}O_2$.) The significance of this

will become clear in our study of digestion, when we find that fats must be broken into their constituents, glycerine and fatty acids, before they can be absorbed. All fats contain glycerine, but they differ in the kind of fatty acid attached to it.

The fats, like carbohydrates, serve as fuel in the body. However, they constitute a reserve supply of energy and are used only after the supply of carbohydrates has been exhausted. Fats yield more than twice as much energy per gram as carbohydrates and thus are a more economical form for the storage of food reserves. But they are not so readily oxidized to release energy, so that the body needs two storage mechanisms: glycogen, which is readily changed into glucose and oxidized, thus serving as a source of energy between meals; and fats, which are a more permanent storage compound, drawn upon only after the glycogen has been used up. Carbohydrates can be transformed by the body into fats and stored—a restatement of the generally known fact that starches and sugars are fattening. To some extent, the reverse may occur: fats or parts of the fat molecule may be converted into glucose.

Fats are a more important structural element of the body than are carbohydrates. The plasma membrane around each cell contains fatty substances as an important constituent, and the myelin sheath around the nerve fibers is made of fats. Fat is deposited in large amounts just under the skin, where it serves as an insulator against the loss of body heat. Whales, which live in cold water and have no insulating hair, have an especially thick layer of fat (blubber) just under the skin for this purpose. A certain amount of subcutaneous fat in man is necessary to keep the skin firm.

Besides the true fats, a number of related fatlike substances have properties similar to them, but contain other things in addition to fatty acids. One of these, the phospholipids, is an important component of nerves.

Proteins. The proteins are compounds containing carbon, hydrogen, oxygen, nitrogen and usually sulfur and phosphorus, in which the characteristic element is nitrogen. Proteins are always present in protoplasm and are much more important as its raw material than are carbohydrates or fats.

Proteins are extremely complex substances, their molecules being by far the largest, most complicated and most varied of all the components of protoplasm. Thousands of atoms are present in each molecule of a protein. A typical protein, of great importance to the human body, is **hemoglobin,** the material responsible for the color of red blood cells. Some idea of the complexity of the hemoglobin molecule can be gained from its formula: $C_{3032}H_{4816}O_{872}N_{780}S_8Fe_4$. (Fe is the symbol for iron.)

Proteins are made of simpler components, known as **amino acids.** At present, thirty-five different amino acids have been found as the result of the chemical breakdown of proteins; the existence of twenty-five of these has been confirmed by further investigations. Since each protein contains perhaps hundreds of amino acids combined in various proportions, there is an almost infinite variety of proteins. Not all proteins contain all the possible amino acids; some have only a few types.

There is a great variety of proteins in each person, and probably each organ has a number of proteins peculiar to it. Finally, it is believed that every species of plant and animal has certain proteins in its protoplasm different from those of any other species. The degree of difference in the proteins of two species depends upon the evolutionary relationship of the forms involved. Organisms less closely related by evolution have proteins which differ more markedly. Investigations of the similarities and dissimilarities of the proteins of organisms have been useful in studies of evolution and have added strong confirmatory evidence to ideas of evolutionary relationships derived from other facts. This generalization is known as the theory of **species specificity**: the protoplasm of each species, due to its constituent proteins, is specific for the species, differing at least slightly from that of related species and markedly from that of more distantly related species. Because of this, grafts of tissue taken from one species of animal usually will not grow when im-

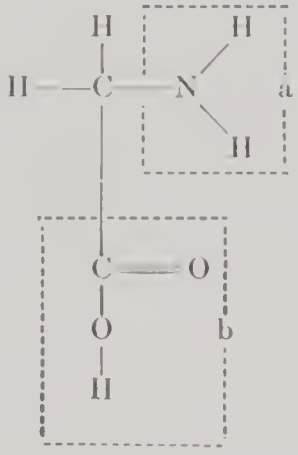


Fig. 6. The structural formula of glycine, the simplest amino acid, showing, *a*, the amino group and, *b*, the acid (carboxyl) group.

planted into a host of a different species, but degenerate and are resorbed by the host.

The structural units of proteins, the amino acids, differ in the number and arrangement of their constituent atoms, but all contain an amino group (NH_2) and an acid group (COOH), whence their name (Fig. 6). The amino group enables the amino acid to act as an alkali and combine with acids; the acid group enables it to act as an acid and combine with alkalis. Amino acids are linked together to form proteins by a connection between the amino group of one and the acid group of another. Pure amino acids derived from proteins have a sweet taste. When proteins are eaten, they are broken up into amino acids in the digestive tract before they can be absorbed into the blood stream. They are then carried to all parts of the body to be made into new protein.

The large size of the protein molecules causes them to form colloidal solutions in water which are the basis of the colloidal nature of protoplasm. When more is known of the chemistry of these extremely complex substances, we shall be closer to an understanding of the activities which constitute life. Although proteins are important in the body chiefly as the structural components of protoplasm, and as the functional constituents of enzymes and certain hormones, they may be used

as fuel for the liberation of heat and energy. Most diets include more protein than is necessary for the maintenance of protoplasm. The excess amino acids lose their amino group (a process called **deamination**), which reacts with other substances to form **urea**, and is excreted; the rest of the molecule, by a rearrangement of the atoms, may be changed into glucose and either used immediately as fuel or stored as glycogen. In prolonged fasting, after the glycogen and stored fats are exhausted, the proteins from protoplasm itself may be used as fuel. The evidence available at present indicates that the human body (and animal protoplasm in general) can manufacture some, but not all, of the amino acids if the proper raw materials are present. Those which cannot be built by the animal body must be obtained directly or indirectly from plants as food. Plants can synthesize all the amino acids from simpler substances. The amino acids which animals cannot synthesize, but must obtain from plants, are known as "essential amino acids."

In summary, the carbohydrates, fats and proteins constitute the bulk of protoplasm. Carbohydrates and fats have only a small role in the structure of protoplasm, but are important as sources of fuel; carbohydrates are readily available fuel; fats are the more permanently stored supplies of energy. Proteins are most important as structural and functional constituents of protoplasm, but may serve as fuel after deamination. The body can convert each of these substances into the others to some extent; its ability to manufacture proteins from carbohydrates or fats is limited.

III. CHARACTERISTICS OF LIVING THINGS

Various biologists, experimenting to understand the nature of life, have drawn up lists of characteristics which all living things seem to exhibit. Although there is not complete agreement about every quality or capacity suggested, the following are generally accepted as the distinguishing features of life; that is to say, all known living organisms have all these qualities, but nonliving objects, though they may exhibit one or two, never have all of them.* We may say, then, that to **metabolize**, to **move**, to **grow**, to **reproduce**, to **adapt** to the environment, and to have **organization** is to be alive. Specific and definite as this list seems, the line between the living and the nonliving is tenuous in some instances; and with certain borderline organisms, such as viruses, it is difficult to determine whether life is present or not.

Most present-day biologists agree that vital phenomena, though more complex, are reducible to the same basis as nonliving phenomena, that both are explainable in terms of chemistry and physics. This is called the **mechanistic** theory. A corollary of this view is that if we knew everything about the chemistry and physics of vital phenomena, we would be able to synthesize life. An opposing school of thought, **vitalism**, states that some unique force, not reducible to the terms of chemistry and physics, controls the activities of life and differentiates living from nonliving things. Vitalists believe that no matter how great our knowledge

* For example, crystals in a saturated solution may "grow"; certain nonliving objects move.

of the physics and chemistry of protoplasm may be, we shall never understand life or be able to create it artificially.

4. Metabolism. Correlated with the fact that the chemical substances present in protoplasm are exceedingly complex is the fact that the chemical reactions which occur in protoplasm are correspondingly complicated. The sum of all the chemical activities of protoplasm which provide for its growth, maintenance and repair is called **metabolism.** Living protoplasm is constantly altering by taking in new substances, changing them chemically in various ways, building new protoplasm, and changing the potential energy contained in large molecules of proteins, carbohydrates and fats into kinetic energy and heat as these substances are changed into other, simpler substances. This constant change of energy is one of the unique and characteristic processes of living things. Some kinds of protoplasm metabolize at a high rate; others, such as seeds and spores, have an extremely low, barely detectable metabolic rate. Even within a particular species or person metabolism may vary, depending upon such factors as age, sex and general health, amount of endocrine secretion, and pregnancy.

The chemical reactions characteristic of life may be divided into two main phases. The term **anabolism** refers to those chemical processes in which simpler substances are united to form more complex substances, resulting in the storage of energy and the manufacture of new protoplasm and growth. **Catabolism** refers to the breaking down of the complex substances resulting in the release of energy and the wearing out and using up of protoplasm. Both types of change occur continuously; indeed, life processes are an intricate combination of the two. Complex compounds are often broken down and then the parts recombined in new ways to form different substances. The interconversion of fats, proteins and carbohydrates would be examples of combined catabolism and anabolism. In young organisms during the growth period, anabolism exceedes catabolism; at maturity, the two are just about equal; in old age, catabolism exceeds anabolism.

Both plant and animal metabolism have anabolic and catabolic phases. Plants, however (with some exceptions), have the ability to manufacture their own organic compounds out of inorganic materials in the soil and air; animals depend on plants for food.

5. Catalysis. Chemists have been able to duplicate a few of the metabolic reactions, usually by means of high temperatures, high pressures, acids or alkalis—agents which protoplasm cannot use to effect metabolic changes, since it would be destroyed by them. In nature the various chemical reactions are brought about by special agents called **enzymes.** These belong to the group of substances known as **catalysts,** which regulate the speed at which a chemical reaction occurs without themselves taking part in the reaction or being consumed as a result of it. Almost any substance may be a catalyst. Water is an excellent one. Thus pure, dry hydrogen gas and chlorine gas may be mixed together without result, but if the slightest amount of water is present, they react with explosive violence to form hydrogen chloride. Finely divided metals—iron, platinum, palladium, and so on—are catalysts widely used in industrial processes. Enzymes are simply one particular kind of

catalyst, namely, protein eatalysts produeed by living eells. Every plant and animal eell contains hundreds of different enzymes, eaeh of whieh eatalyzes a partieular reaetion. Most enzymes eontrol a single reaetion under one set of conditions, and exaetly the opposite reaetion under another set. For example, one plant eell enzyme ehanges stareh to sugar at low temperatures and sugar to starch at higher temperatures. Most enzymes remain and perform their funetions within the cell where they were synthesized, but a few—notably thosc coneernod in digestion—operate outside the cell of their origin.

Little was known of enzymes until the latter part of the nineteenth century, when, after a prolonged argument between Louis Pasteur and a German named Liebig as to whether or not they were living things, another German, Büehner, extraeted an enzymc from yeast. He found that the liquid filtered off from erushed yeast eells would ehange stareh to sugar as the living yeast would. Because he was unable to identify the active chemical substance in his filtrate he ealled it an enzyme ("in yeast"). Since then many other enzymes have been identified and much has been learned of enzymatic activity.

Most enzymes are soluble in water and under proper eonditions may be removed from cells. By careful evaporation they may be obtained in the dry state and kept for long periods of time while retaining their ability to catalyze. They act over only a limited range of temperaturc, and most are destroyed by boiling. They are also sensitive to the presence of acids and alkalis. About thirty-five enzymes have been isolated as pure erystalline substances so far, and all have proved to be proteins; probably all enzymes are proteins. Enzymes are named by the type of ehemical reaction they eatalyze. Proteolytie enzymes break down (and probably build up) proteins; hydrolytic enzymes break down substanees by making them combine with water, or build up substanees by removing a molecule of water from two simpler moleeules. Two moleeules of glucose ($C_6H_{12}O_6$) may be eombined by the removal of a moleeule of water to form a single moleeule of suerose, $C_{12}H_{22}O_{11}$. Enzymes are not living, but are indispensable to protoplasm beeause they enable it to metabolize under eonditions of temperature, pressurc and acidity which do not destroy it. Almost without exeeption, the chemieal reactions fundamental to movement, growth, reproduction, irritability and adaptation are controlled by enzymes.

6. Movement. Obvious movement by the higher animals is not the only kind whieh oeeurs in the world of life. The motion of plants and some of the lower animals may be visible only when magnified by the microscope, but it is going on eonstantly. All life exhibits it, even though in some simple organisms it is restrieted to the streaming of protoplasm inside the cell.

7. Growth. Growth, another charaeteristie of living things, is really the result of anabolism. An increasc in the size of an animal or plant may be produeed by an increase in either the sizc or number of the fundamental units of protoplasm (eells). Somc organisms—most trees, for example—will grow indefinitely. But most animals havc a definite growth period which terminates in a partieular adult sizc eharaeteristic of the species.

8. Reproduction. That living organisms are further differentiated from nonliving things by their ability to reproduce their kind is expressed by one of the fundamental tenets of biology: "All life comes only from living things." For centuries it was generally believed that many types of life could arise spontaneously from nonliving things—that frogs and rats arose each spring from the mud of the Nile, for example. The classical experiment disproving the idea of the spontaneous generation of life was performed by the Italian, Francesco Redi, about 1680. It was generally believed at the time that maggots came from decaying meat. Redi proved that they did not by the following simple experiment. He placed a piece of meat in each of three jars. One of the jars was left uncovered, one was covered with fine gauze, and the third was covered with parchment. All three pieces of meat decayed. Maggots appeared on the meat in the uncovered jar, a few maggots appeared on the gauze of the second jar, but not on the meat, and no maggots were found on the meat covered with parchment. Redi demonstrated that the maggots did not come from the decaying meat, but hatched from eggs laid by blow flies attracted by the smell of the decaying meat. The gauze covering permitted the odor of decay to escape and attract the flies, which laid their eggs on the gauze. Further observations showed that the maggots developed into flies which in turn laid more eggs.

With the discovery of bacteria the question of the spontaneous origin of these tiny organisms was raised. Many experiments were performed before Pasteur finally demonstrated that bacteria, too, come only from previously existing bacteria. The comparatively recent discovery of the extremely small filterable viruses has suggested to some biologists that perhaps these organisms arise from nonliving material. Although the question has not been settled, most biologists believe that even the viruses come only from previously existing viruses.

9. Adaptation. The ability of plants and animals to adapt to their environment is the characteristic which enables them to remain alive through the exigencies of a changing world. Adaptation depends upon the *irritability* of protoplasm, its ability to receive stimuli of various kinds from its surroundings. The stimuli may be thermal, electrical, chemical or mechanical, but the kind of response depends upon the properties of the protoplasm stimulated. Sometimes an organism adapts simply by moving away from a harmful stimulus. If the tiny single-celled organisms known as paramecia (Fig. 85) are placed in a tube of water heated at one end and iced at the other, the animals will adapt by moving to the center of the tube. They do this, not by any rational process, but by trial and error, moving in one direction until some unfavorable condition is encountered, then backing up and going in a different direction.

Plants cells also are sensitive to changes in their environment, although their responses are not always so apparent as those of animals. The flowing of protoplasm in the plant cell may be speeded up or stopped by external changes. A few plants, such as the Venus flytrap, which grows in many swamps, have a remarkable sensitivity to touch and catch insects. Their leaves are hinged along the midrib (Fig. 7), and the edges of the leaves are covered with hairs. When an insect lights

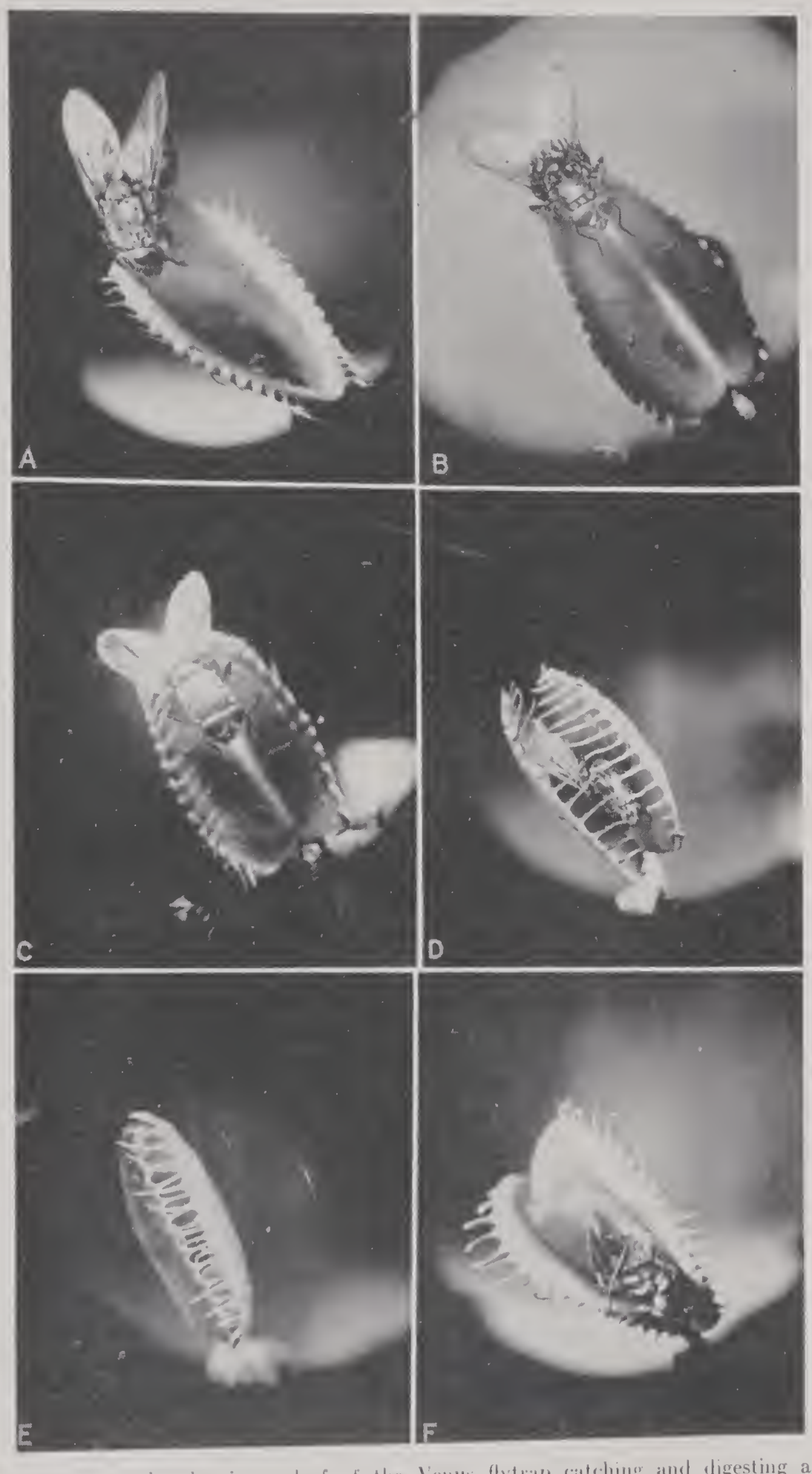


Fig. 7. Photographs showing a leaf of the Venus flytrap catching and digesting a fly. (Copyrighted by the General Biological Supply House, Chicago.)

on the leaf, the edges come together after a few seconds and the hairs interlock to prevent its escape. The leaf then secretes substances which kill and digest the insect. The development of this fly-trapping mechanism is an adaptation to the fact that the soil in which the plant grows is poor in nitrogen. These plants obtain part of their nitrogen from the prey they "eat."

10. Specific Organization. Because living things are not homogeneous throughout their structures, but are made of different parts, each with special functions, *specific organization* is one of their outstanding characteristics. The individual units are systematically coordinated to form a complete, active organism. The bodies of the higher animals, including man, are organized in a series of increasingly complex levels: cells are organized into tissues, tissues into organs, and organs into organ systems. The organization of plants differs in detail, but is similar in principle.

QUESTIONS

1. Explain why water is essential to protoplasm.
2. State the particular functions in the body of the three main types of protoplasmic organic compounds.
3. Why can we be sure that the first living things were plants and not animals?
4. What is the importance of enzymes in the body?
5. Discuss the characteristics of living things. Can you think of any which should be added to the list? Any which do not seem essential?
6. Are you inclined to believe the vitalistic or the mechanistic theory? Why?

SUPPLEMENTARY READINGS

Gerard, R. W.: *Unresting Cells*. New York, Harper & Brothers, 1940.
A less-advanced discussion of some of the chemical aspects of protoplasm.

Heilbrunn, L. V.: *An Outline of General Physiology*. 2d ed. Philadelphia, W. B. Saunders Company, 1943.
A detailed, advanced discussion of the physicochemical nature of cytoplasm.

Moulton, F. R. (editor): *The Cell and Protoplasm*. Lancaster, Pa., The Science Press, 1940.
A collection of interesting, readable short papers on a variety of topics related to protoplasm, by a group of authorities in the field.

CHAPTER 4

CELLS AND TISSUES

I. CELLS

THE PROTOPLASM of the human body and of all plants and animals is nowhere present in a single large mass, but exists in tiny discrete portions called **cells.** These are the units of structure of the body, just as bricks may be the units of structure of a house. But they are more than mere building blocks; each is an independent, functional unit, and the processes of the body are the sum of the coordinated functions of its cells. The units vary considerably in size, shape and function. Some plants and animals have bodies made of just a single cell; others, such as a man or an oak tree, are made of countless billions fitted together.

The term "cell" was first used in 1665 by Robert Hooke, in his ac-

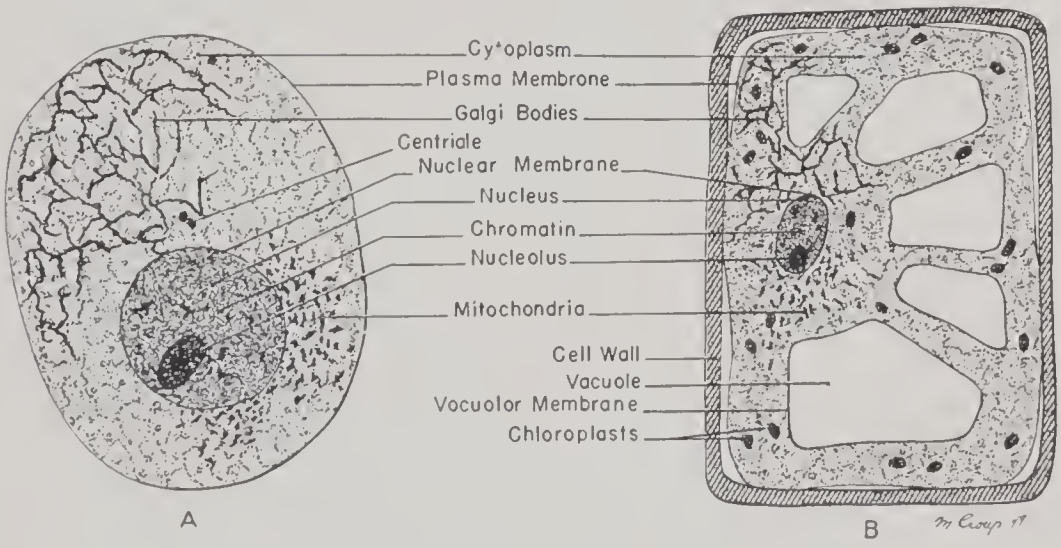


Fig. 8. Diagrams of a typical animal cell, *A*, and plant cell, *B*.

count of a study made with the newly invented microscope. He applied the term originally to the tiny, boxlike cavities he observed in a piece of cork. Now we know that what he saw were the walls of dead cells, and that the important part of the cell is its contents. In 1839 a Czech, Purkinje, introduced the term **protoplasm** for the living contents of the cell. About the same time two Germans, Schleiden, a botanist, and Schwann, a zoologist, formulated the generalization since known as the cell theory: the bodies of all plants and animals are composed of cells which are the fundamental units of life. These men were in error about a number of details, but their generalization has been proved correct. Such a statement was possible only after years of microscopic observation.

Although cells vary in many aspects, they all have several features in common (Fig. 8):

(*a*) Cells are completely encircled and enclosed by a **plasma membrane,** which is made of protoplasm and is a living, functional part of

the cell, extremely important in regulating its contents. All food entering the cell and all waste products or secretions leaving it must pass through this membrane. Nearly all plant cells (but not most animal cells) have a thick **cell wall** made of cellulose, outside of and in addition to the plasma membrane. This cell wall is generally regarded as nonliving, a secretion of the protoplasm. The cell wall is pierced in many places by tiny holes, through which the protoplasm of one cell connects with that of the adjacent cells. Through these perforations, materials can pass from one cell to another. The cell walls are important in providing the body of the plant with support.

(*b*) Each cell contains a small, usually spherical, body known as the **nucleus.** In some cells this has a fixed position, usually near the center; in others it may move around freely. The nucleus is the controlling center, directing cellular activity and containing the factors responsible for the inheritance of the traits of the animal or plant. The protoplasm of the nucleus is called **nucleoplasm.** If a cell is cut in half with a microdissection apparatus, so that one half contains the nucleus and the other half lacks it, the half with the nucleus continues to live, but the anucleate fragment invariably dies.

Hämmerling, using the single-celled plant, *Acetabularia*, performed some interesting experiments demonstrating the importance of the nucleus in controlling the growth of the cell. This marine alga, which may be as large as 5 cm., superficially resembles a mushroom, having a stalk and "roots," surmounted by a large, disc-shaped umbrella. The whole plant is one cell and has only one nucleus, located near the base of the stalk. Hämmerling cut the stem (Fig. 9) and found that the lower part could regenerate an umbrella and live. The umbrella part, which had no nucleus, lived for a considerable time, but eventually died without being able to regenerate the lower part. In a second type of experiment, Hämmerling first cut off the nucleus from the stem (cut 1, Fig. 9), then removed the umbrella from this fragment (cut 2), isolating a piece of stem. This section was able partially or completely to regenerate the umbrella. When this second umbrella was cut off (cut 3), the stem was unable to regenerate another umbrella. These and similar experiments showed that the nucleus gives off a substance necessary for umbrella regeneration, which diffuses up the stem. After cuts 1 and 2 some of this substance remained in the stem, although, of course, the stem received no additional material from the nucleus. This substance is exhausted in producing the first umbrella or simply diffuses out of the cut ends of the stem, so that the latter is unable to regenerate a second umbrella if the first is removed (cut 3). This is one of the clearest examples of the production by the nucleus of a substance which regulates cell growth.

(*c*) The membrane separating the nucleus from the surrounding protoplasm is called the **nuclear membrane;** like the plasma membrane, it is made of protoplasm. It regulates the constant flow of materials in and out of the nucleus.

(*d*) In a living cell the protoplasm of the nucleus usually appears homogeneous, but when the cell has been killed and stained, a number of structures are visible. Running irregularly through the nucleus are strands of **chromatin,** a substance which has a special affinity for certain

dyes, and stains deeply. At the time of cell division these chromatin threads form the **chromosomes,** rod-shaped bodies which bear the hereditary units, the **genes.** The **nucleolus** is a spherical body found within

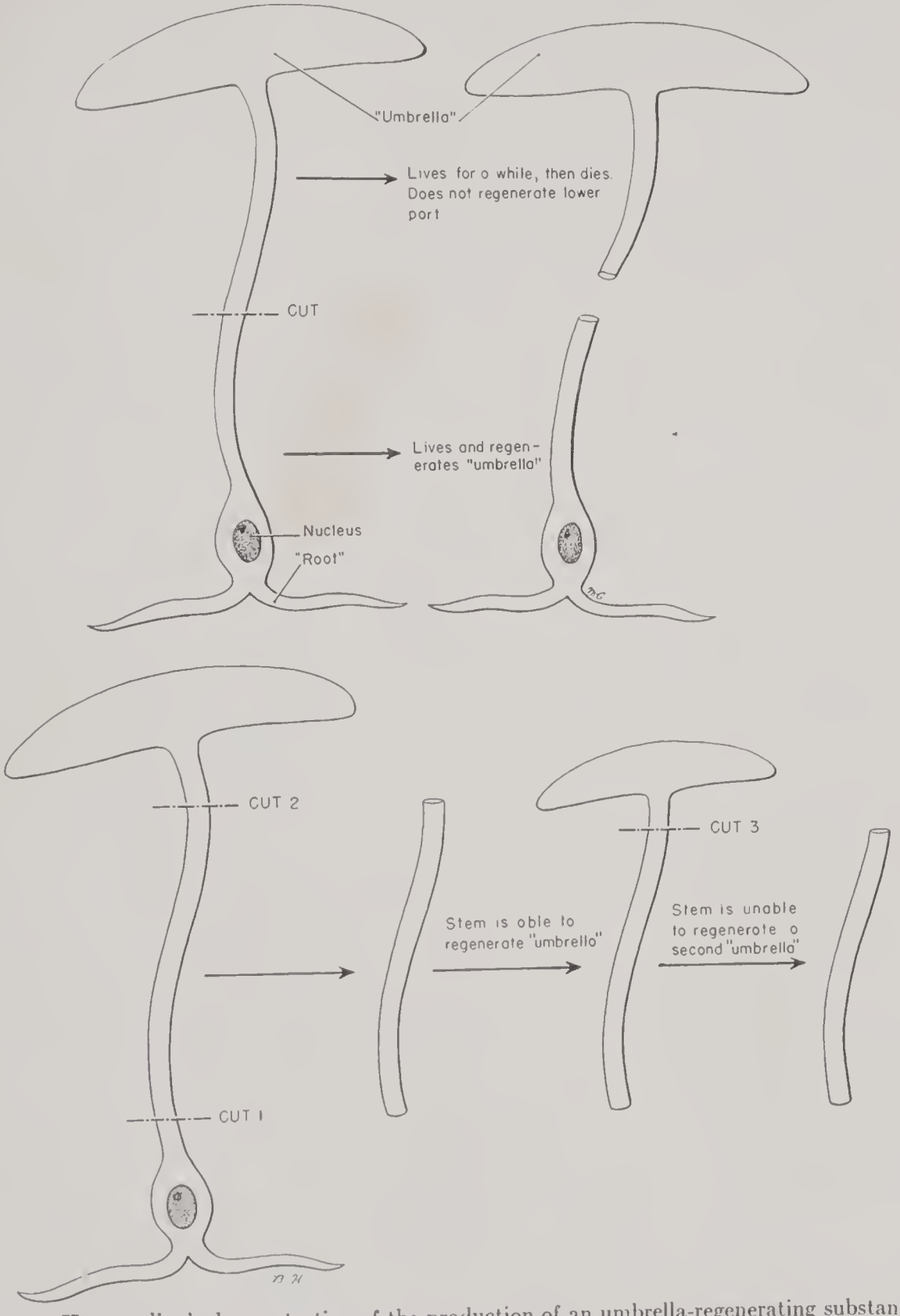


Fig. 9. Hämmerling's demonstration of the production of an umbrella-regenerating substance by the nucleus of *Acetabularia.* See text for discussion.

the nucleus. It is extremely variable in some cells, appearing and disappearing, changing its form and structure. The nucleus may contain one or more of these. The function of the nucleolus is not well under-

stood; apparently, it has something to do with cell division, since it disappears during that process and reappears afterwards.

(*e*) The protoplasm outside the nucleus is called **cytoplasm.** In some cells—for example, in the single-celled animal, *Ameba*—the cytoplasm has two more or less distinct parts: an outer, clear **ectoplasm,** and an inner, granular **endoplasm.** In most cells this division is not visible. The cytoplasm contains specialized structures to perform specific functions. Some of these inclusions are centrioles, plastids, mitochondria and Golgi bodies.

Within the cytoplasm of animal cells, lying near the nucleus, is a small, dark-staining inclusion, the **centriole.** The cells of higher plants lack these bodies, although the lower plants have them. The centriole is active at the time of cell division (see Chap. 23), but it cannot be absolutely essential for cell division, since plant cells divide without it.

All plants, except fungi, have small protein bodies called **plastids** in the cytoplasm. One type of plastid, called a **chloroplast,** contains the pigment chlorophyll, which is responsible for the green color of plants and is of paramount importance in the manufacture of food. A second type of plastid are colorless bodies, the **leukoplasts,** which are believed to act as centers for the storage of materials in the cytoplasm. A third type, **chromoplasts,** may be any color and are responsible for the color of flowers and fruits.

Almost all cells have in their cytoplasm tiny bodies, known as **mitochondria,** which may appear as threads, granules or rods. These bodies may rapidly change their size, appearance and position in the cell, usually being most numerous in the part of the cell with the highest metabolic rate. They are believed to consist of phospholipids and proteins and to be concerned with the regulation of the oxidation rate in the cell. In plants, mitochrondria are found in clusters at the point of formation of the plastids and are believed to be involved either directly or indirectly with the formation of those bodies. Mitochondria can be recognized by the fact that they are stained selectively by a particular stain, Janus green.

Golgi bodies, another type of living inclusion, are found in the cytoplasm of all cells except mature sperm and red blood cells, and are believed to be neeessary for the synthesis of proteins, especially enzymes. They, too, may appear as granules, threads or rods, or as canals, and are distinguished from mitoehondria by the fact that they stain with neutral red instead of Janus green. Dr. Beams, using the ultraeentrifuge, showed that mitochondria are heavier than protoplasm and that Golgi bodies are lighter.

Besides these living elements, cytoplasm may contain vacuoles or cavities filled with a watery liquid and separated by a vacuolar membrane from the cytoplasm. Vacuoles are common in the cells of plants and lower animals, but rare in those of higher organisms. Most protozoa have **food vacuoles,** containing food in the process of being digested, and **contractile vacuoles,** which pump excess water out of the cell. Finally, cytoplasm may contain granules of storcd starch or protein or droplets of oil.

There are three main differences between animal and plant cells:

animal cells, but not the cells of higher plants, have a centriole; plant cells, but not those of animals, have plastids in the cytoplasm; and plant cells have a stiff cell wall of cellulose which prevents their changing position or shape, while animal cells usually have only the thin plasma membrane and thus are able to move and alter in shape.

All cells show certain basic similarities in their metabolism. They all carry on oxidation, breaking down glucose and other compounds to release energy, and they all build up protoplasm and manufacture certain basic cell enzymes. Superimposed on these basic functions, common to all of them, may be certain other activities peculiar to a particular type: thyroid gland cells manufacture thyroxin, cells in the lining of the stomach produce pepsin, muscle cells contract, and so on.

To study the details of cell structure, bits of tissue must be killed, cut in thin sections with a mechanical device known as a microtome, and stained with dyes. Since the nucleus, cytoplasm, mitochondria, Golgi bodies and other parts are chemically different, they combine with different stains. The stained slices of tissue are then mounted on glass slides, covered with another piece of glass and observed under the microscope. In the last thirty years many new facts about cell function and structure have been discovered by observing and photographing **tissue cultures.** The method of making tissue cultures consists in preparing and sterilizing a special nutritive material and then placing it in a small cavity in a sterile glass slide. With it is placed a bit of living tissue, and the solution is sealed under a piece of glass. The tissue will live indefinitely if the medium is renewed and oxygen is supplied; cells from a chick's heart have been kept alive in a New York laboratory since 1912. Apparently cells in tissue culture do not grow old. Those from a sarcoma (a type of cancer) grow with unusual vigor in tissue culture, and they grow more rapidly in the blood plasma of a healthy person than in that from an animal with sarcoma. It appears that the sarcoma cells in the body stimulate some of the healthy cells to manufacture a substance which inhibits the malignant growth to some extent. A recent advance in the technique of tissue culturing is the invention of devices such as the Lindbergh-Carrel mechanical heart for the circulation of fresh medium and oxygen to the growing tissue without breaking the sterile seal. The medium consists of blood plasma, an extract of embryonic tissues and, sometimes, added vitamins and other chemicals.

II. ANIMAL TISSUES

When numbers of similar, specialized cells are grouped together, they are able to perform complex functions and are known as **tissues.** It is important, however, to remember that tissues may consist of more than living cells. Connective and vascular tissues, for example, contain some nonliving material between the cells.

Biologists differ in their opinions of how the various types of tissue should be classified and, consequently, of how many main types of tissue there are. We shall classify animal tissues according to six main types: epithelial, connective, muscular, vascular, nervous and reproductive.

1. Epithelial Tissues. Epithelial tissues are composed of cells which form a layer or sheet covering the body surface or lining the body cavi-

ties. They have one or more of the following functions: **protection, absorption, secretion** and **sensation.** The epithelia of the body protect the underlying cells from mechanical injury, from harmful chemicals and bacteria, and from drying. The epithelia lining the digestive tract absorb food and water into the body. Other epithelia give off a wide variety of substances as waste products or for use elsewhere in the body; finally, since the body is entirely covered by epithelium, it is obvious that all sensory stimuli must penetrate an epithelium to be received. Examples of epithelial tissue are the outer layer of the skin, the lining of the digestive tract, the lining of the windpipe and lungs and the lining of the kidney tubules. Epithelial tissues are divided into six subtypes according to their shape and function:

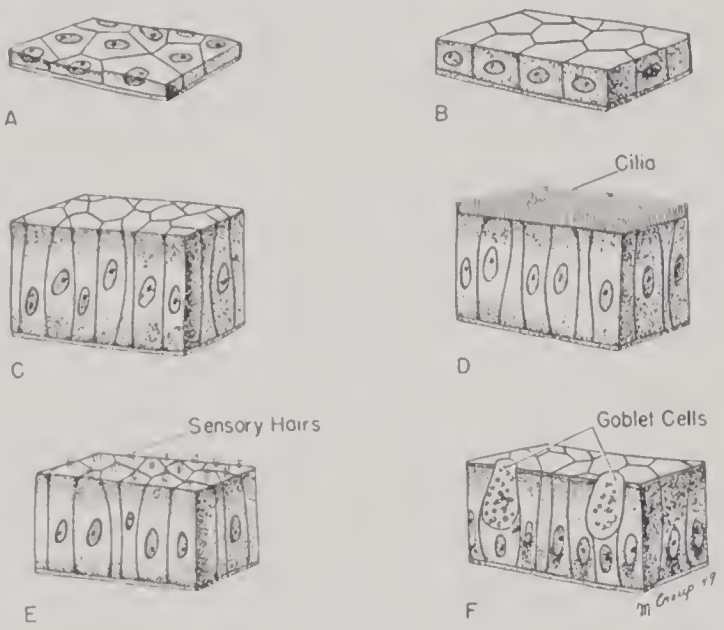


Fig. 10. Types of epithelial tissue. *A*, Pavement epithelium; *B*, cuboidal epithelium; *C*, columnar epithelium; *D*, ciliated columnar epithelium; *E*, sensory epithelium (cells from the lining of the nose); *F*, glandular epithelium: two single-celled glands ("goblet" cells) in the lining of the intestine.

Pavement epithelium cells are flattened, having the shape of pancakes or flagstones (Fig. 10, *A*). Such tissue occurs on the surface of the skin and the lining of the mouth, esophagus and vagina. In man and the higher animals, pavement epithelium usually occurs as several layers of these flat cells piled on top of each other, a condition called stratified pavement epithelium.

Cuboidal epithelium cells are cube-shaped, resembling dice (Fig. 10, *B*). This tissue lines the kidney tubules and the urinary bladder.

Columnar epithelium cells are elongated, resembling pillars or columns; the nuclei are usually located near the base of the cell (Fig. 10, *C*). The stomach and intestine are lined with columnar epithelium.

Ciliated epithelium (Fig. 10, *D*). Columnar cells may have on their free surface small protoplasmic projections called **cilia,** which beat rhythmically and move materials in one direction. Most of the respiratory system is lined with ciliated columnar epithelium whose cilia beat in order to bring any foreign material which may get into the system back to the mouth.

Glandular epithelium cells (Fig. 10, *E*) are specialized to secrete sub-

stances such as milk, wax or perspiration. They are either columnar or cuboidal in shape.

Sensory epithelium cells (Fig. 10, *F*) are specialized to receive stimuli. The cells lining the nose—the olfactory epithelium, responsible for the sense of smell—are an example.

2. Connective Tissue. Connective tissue, which includes bone, cartilage, tendons, ligaments and fibrous connective tissue, supports and holds together the other cells of the body. The cells of these tissues characteristically secrete a large amount of nonliving material, called **matrix**, and the nature and function of the particular connective tissue is determined largely by the nature of this intercellular substance. The

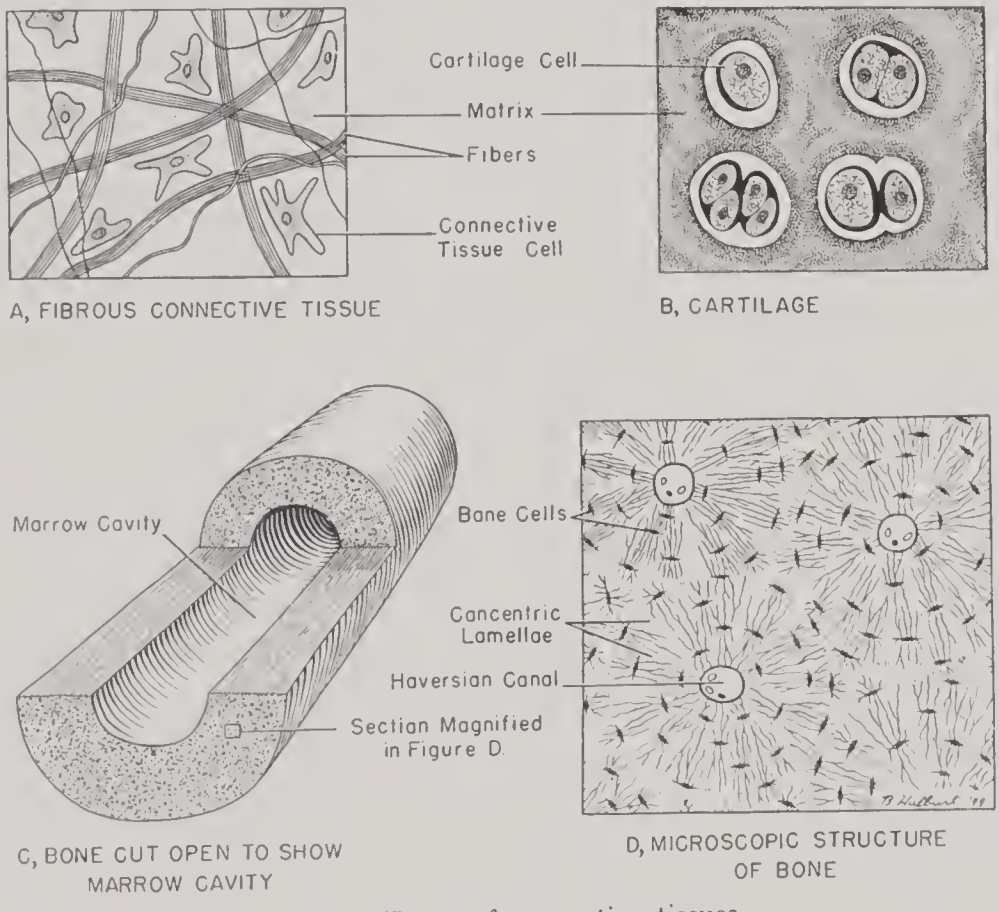


Fig. 11. Types of connective tissues.

cells thus perform their functions indirectly by secreting a matrix which does the actual supporting or connecting.

In **fibrous connective tissue** the matrix is a thick, interlacing, matted network of fibers secreted by and surrounding the connective tissue cells (Fig. 11, *A*). Such tissue occurs throughout the body and holds skin to muscle, keeps glands in position and binds together many other structures. Tendons and ligaments are specialized types of fibrous connective tissue. **Tendons** are not elastic and connect muscles to each other or to bone. **Ligaments** are somewhat elastic and connect one bone to another. There is an especially thick mat of connective fibers just below the skin. When this is treated chemically (tanned) it becomes leather. It would be possible to make leather from human tissue; indeed, in some primitive tribes it was quite the thing to "tan the hide" of one's enemy and make a pair of gloves.

In some of the lower animals the entire skeleton is made of **cartilage** or **gristle;** in higher animals most of the cartilage has been replaced by bone. In the human body, cartilage may be felt in the supporting structure of the ear flap (pinna) and in the tip of the nose. It is firm yet elastic. Cartilage cells secrete this hard, rubbery matrix around themselves and come to lie in groups of one, two or four, in small cavities in the homogeneous, continuous, matrix (Fig. 11, *B*). The cartilage cells imbedded in the matrix remain alive; some of them secrete fibers which become imbedded in the matrix and strengthen it.

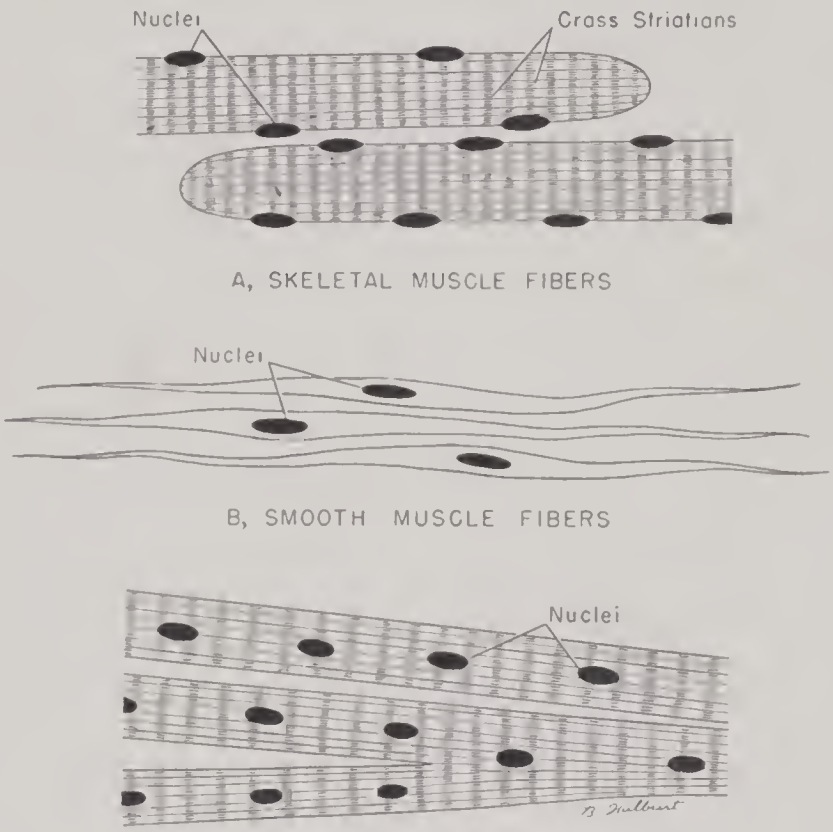


Fig. 12. Types of muscle tissue.

Bone cells remain alive and secrete a bony matrix throughout a person's life. The matrix contains calcium salts and organic matter which are responsible for hardness and lack of brittleness, respectively, enabling bone to stiffen and support the body against the pull of gravity. The bones of elderly people have more calcium and less organic matter than those of young people, and for this reason are more brittle. Contrary to appearances, bone is not a solid structure. Most bones have a large cavity, the **marrow cavity,** in the center (Fig. 11, *C*). Running through the matrix of the bone are channels (Haversian canals) in which lie blood vessels and nerves to supply and control the bone cells. The bone matrix is secreted in concentric rings (lamellae) around the canals, and the cells become imbedded in cavities in these rings (Fig. 11, *D*). Bone cells are connected to each other and to the Haversian canals by tiny tubes, through which they obtain oxygen and nourishment and eliminate wastes. Bones also contain cells which destroy bone, so that they gradually change their shape in response to continued stresses and strains.

3. Muscular Tissues. Muscular tissue is made of cells which have the ability to contract quickly and thus do work. There are three distinct types of this tissue in the human body: **skeletal, smooth** and **cardiac** (Fig. 12). All are made of elongated fibers which become shorter and thicker during contraction. Each fiber contains a number of longitudinal myofibrils. Skeletal and cardiac fibers are exceptions to the rule that cells have only one nucleus: each fiber has many nuclei. The nuclei of skeletal fibers are also unusual in their position, which is peripheral, just under the cell membrane; presumably this is an adaptation to increase the efficiency of contraction. Under the microscope, skeletal and cardiac fibers are seen to have tiny alternate light and dark transverse stripes or striations. These stripes appear to be involved in contraction, for they change their relative sizes during contraction, the dark stripes decreasing and the light stripes increasing in width. Skeletal muscle is sometimes called **voluntary** muscle, because it is under the control of the will. Cardiac and smooth muscles are called **involuntary** because they cannot be regulated by the will. Table 3 summarizes the features which distinguish the three types of muscle tissue.

Table 3. Comparison of the Types of Muscle Tissue

	Skeletal	Smooth	Cardiac
Location	Attached to skeleton	Walls of viscera, stomach, intestines, etc.	Wall of heart
Shape of fiber	Elongate, cylindrical, blunt ends	Elongate, spindle-shaped, pointed ends	Elongate, cylindrical, fibers branch and fuse
Number of nuclei per fiber	Many	One	Many
Position of nuclei	Peripheral	Central	Central
Cross striations	Present	Absent	Present
Speed of contraction	Most rapid	Slowest	Intermediate
Ability to remain contracted	Least	Greatest	Intermediate
Type of control	Voluntary	Involuntary	Involuntary

4. Vascular Tissues. Vascular tissue includes the red and white blood cells and the liquid, noncellular part of the blood, the plasma. Many biologists classify blood with the connective tissues because they originate from similar cells.

5. Nervous Tissue. Nervous tissue is made of cells, called **neurons,** specialized for conducting impulses. Each neuron has an enlarged structure, the **cell body,** which contains the nucleus, and two or more nerve fibers extending from the cell body (Fig. 13). The nerve fibers are made of cytoplasm and are covered by a cell membrane. Some are extremely long—those stretching from the spinal cord down the arm or leg may be 3 feet or more in length. All are microscopic in width. The neurons

are connected together in chains to pass impulses for long distances through the body. Two consecutive neurons do not actually touch as do two strands of copper wire spliced together to carry an electric impulse. Instead, there is a small gap, called a **synapse,** between them, which regulates the transmission of impulses from one neuron to the next. Two types of nerve fibers, **axons** and **dendrites,** are differentiated on the basis of the direction in which they normally conduct a nerve impulse: axons conduct nerve impulses *away* from the cell body; dendrites conduct them *toward* the cell body. Neurons have many sizes and shapes, but all have the same basic plan.

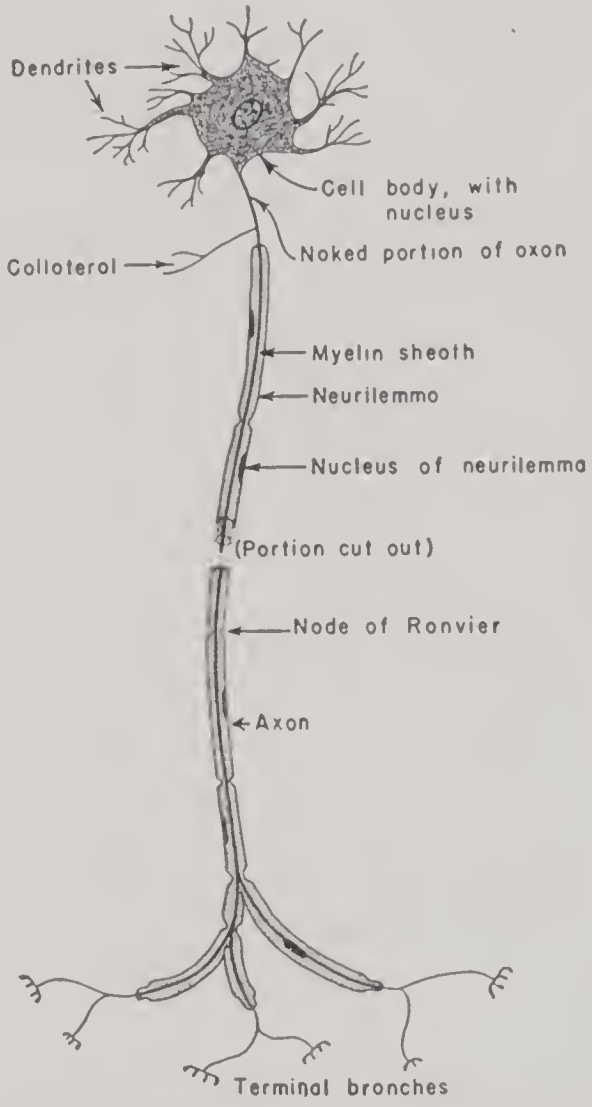


Fig. 13. Diagram of a single neuron. (Hunter and Hunter: College Zoology.)

6. Reproductive Tissue. Reproductive tissue is made up of cells modified to produce offspring—namely, egg cells in females and sperm cells in males (Fig. 14). Egg cells are usually spherical or oval and are nonmotile. The cytoplasm of the egg of most animals, but not of the higher mammals, contains a large amount of yolk which serves as food for the developing organism from the time of fertilization until it is able to obtain food in some other way. Sperm cells are much smaller than eggs; they have lost most of their cytoplasm and developed a tail by which they propel themselves. A typical sperm consists of a **head,** which contains the nucleus, a **middle piece,** and a **tail.** The shape of the sperm varies in different species of animals (Fig. 203). Because eggs and

sperm develop from epithelial-like tissue in the ovaries and testes, some biologists classify them with those tissues.

III. PLANT TISSUES

The cells of the higher plants are also organized and differentiated into tissues. Plant biologists recognize four main types of tissue: **meristematic, protective, fundamental** and **conductive.**

7. Meristematic Tissue. Meristematic tissues are made of small, thin-walled cells which are rich in protoplasm and have few vacuoles (Fig. 15). They are found in the rapidly growing parts of the plant—the buds, root tips and cambium layer.

Fig. 14. Human egg and sperm. *A*, An egg just removed from the ovary, still surrounded by follicle cells. Note the large nucleus and nucleolus. To the left are four sperm, showing relative size (× 400). *B*, Top and side views of a sperm: *h*, head; *m*, middle piece; *t*, tail (× 2000). (Woodruff: Foundations of Biology, The Macmillan Co.)

8. Protective Tissue. Protective tissue consists of cells with thicker walls, such as the epidermis of leaves and the cork layers of stems and roots. Leaves are frequently waterproofed by a waxy material called **cutin,** secreted by the epidermis. The epidermal layer may develop hairs (especially in roots) and scales.

9. Fundamental Tissues. The fundamental tissues make up the great mass of the plant body, including the soft parts of the leaf, the pith and cortex of stems and roots, and the soft parts of flowers and fruits. Their chief function is the storage of food. The simplest of the fundamental tissues is **parenchyma,** in which the cells have a thin wall and a large vacuole (Fig. 16, *A*). In some fundamental tissue the corners of the cells are thickened to help support the plant. Such tissue, called **collenchyma** (Fig. 16, *B*), occurs just beneath the epidermis of the stem. In still another type, known as **sclerenchyma,** the entire cell wall be-

Fig. 15. Photograph of a lengthwise section of an onion root tip, showing meristematic tissue. A number of the cells can be seen in various stages of cell division. (Holman and Robbins: Textbook of General Botany, John Wiley and Sons.)

comes greatly thickened (Fig. 16, *C*), giving stiffness and hardness to the plant. It sometimes occurs as long thin fibers.

There are two types of conductive tissue: **xylem** cells, which conduct water, and **phloem** cells, which conduct food. In all higher plants the first xylem cells to develop are long ones, called **tracheids,** with pointed

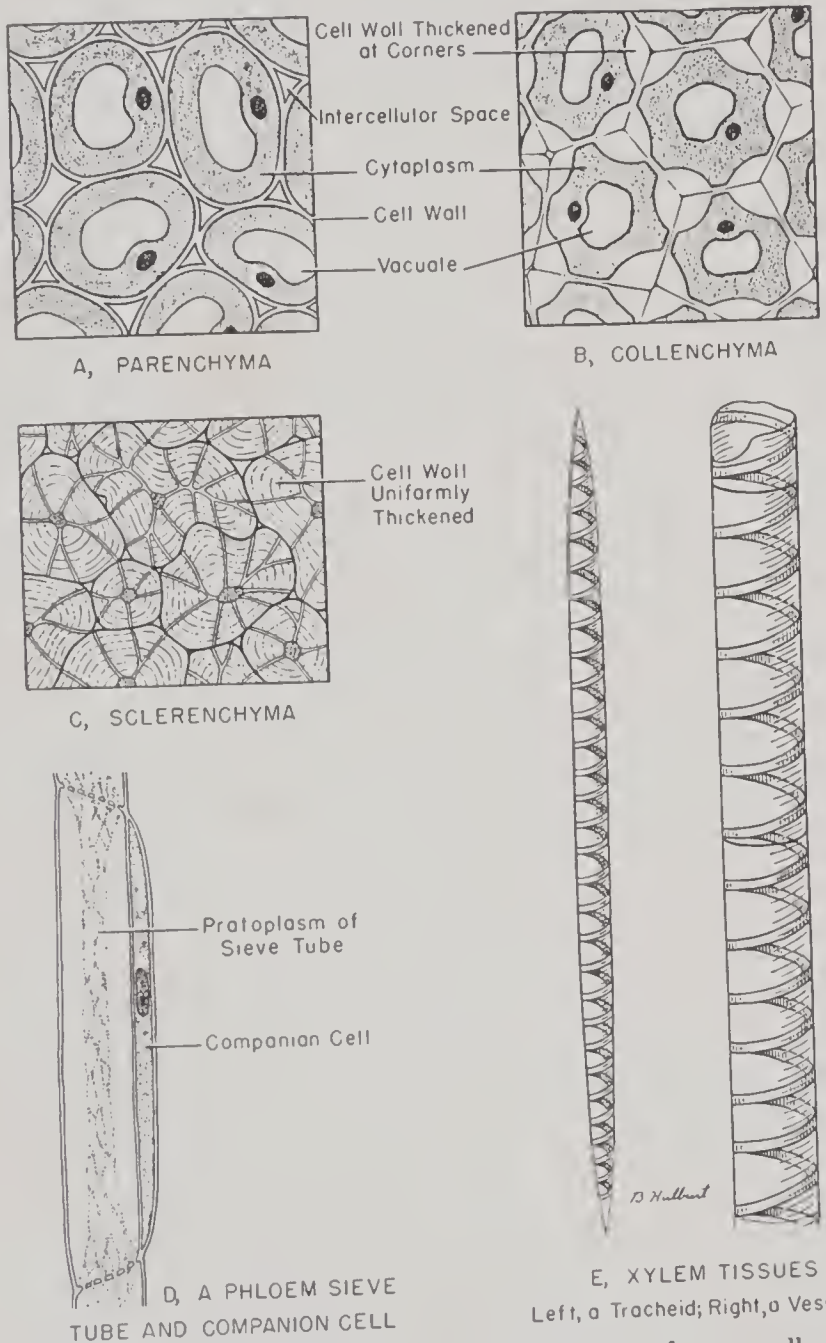


Fig. 16. Some types of plant tissues: protective tissues, parenchyma, collenchyma, sclerenchyma, tracheids and sieve tubes.

ends and thickenings on the walls in a circular, spiral or pitted pattern (Fig. 16, *E*). Later, other cells join end to end to form **xylem vessels.** As the vessels develop, the end walls dissolve and the side walls thicken, leaving a long cellulose tube for the conduction of water. In both tracheids and vessels the cytoplasm eventually dies, leaving the tubes, which continue to function. The thickening, which involves the deposition of **lignin,** the substance responsible for the hard, "woody" nature of plant stems and roots, enables xylem to act as a supportive as well as

a conductive tissue. A similar end-to-end fusion of cells gives rise to the **sieve tubes** of the phloem (Fig. 16, *D*). The ends of the cells do not disappear, but remain as a perforated plate, the sieve plate. The nuclei, but not the cytoplasm, of the phloem cells disappear.

IV. ORGAN SYSTEMS

The bodies of single-celled animals and plants are not, of course, organized into tissues and organs; all the life functions are carried on by the one cell. In more complex organisms a division of labor has occurred and special systems have evolved to perform each of the principal life functions. In man, eleven organ systems are recognized, as follows:

The **circulatory system,** which transports materials around the body.

The **respiratory system,** which provides a means for oxygen to enter, and carbon dioxide to leave, the blood.

The **digestive system,** which takes in food, breaks it up chemically into small molecules, and absorbs it into the blood.

The **excretory system,** which eliminates the waste products of metabolism.

The **integumentary system,** which covers and protects the entire body.

The **skeletal system,** which supports the body and provides for movement and locomotion.

The **muscular system,** which functions with the skeletal system in movement and locomotion.

The **nervous system,** which conducts impulses around the body and integrates the activities of the other systems.

The **sense organs,** which receive stimuli from the outer world and from the various regions of the body.

The **endocrine system,** which is an additional coordinator of the body functions.

The **reproductive system,** which provides for the continuance of the species.

V. BODY PLAN AND SYMMETRY

In referring to parts of the body, biologists use the following terms: **anterior,** referring to the head end of the body; **posterior,** to the tail end of the body; **dorsal,** to the back side; **ventral,** to the belly side; **medial,** to the midline of the body; and **lateral,** to the side. These terms are also used to indicate relative position. For example, the neck is anterior to the chest; the ribs are posterior to the collar bone; the spinal cord is dorsal to the body cavity.

Animal and plant bodies may be organized according to one of three types of symmetry. A body is said to be symmetrical if it is possible to cut it into two equivalent halves. If a body is spherical, and is completely homogeneous, like a rubber ball, so that it is possible to cut it in any plane through the center and get two equal halves, it is said to have **spherical symmetry**. Only a few of the lowest plants and animals have this type of organization. In **radial symmetry** two sides are distinguishable, a top and a bottom, as in a mushroom or a starfish. A mushroom can be cut into two equal halves by any plane which includes the line or axis running through the center from top to bottom. Human beings

and all the higher animals have **bilateral symmetry,** in which only one special cut will divide the body into two equivalent halves. In bilaterally symmetrical animals, anterior, posterior, dorsal and ventral sides can be distinguished. In man, for example, only a plane from head to foot exactly in the center will divide the body into equivalent halves, right and left.

In a bilaterally symmetrical animal, three planes or sections are possible:

Transverse planes, which include a dorsal-ventral axis and a left-right axis, but are at right angles to the anterior-posterior axis.

A **sagittal** plane, which includes the dorso-ventral axis and the anterior-posterior axis, but is at right angles to the left-right axis.

A **frontal** plane, which includes the anterior-posterior axis and the left-right axis, but is at right angles to the dorso-ventral axis.

In learning to differentiate between these body planes, it is helpful to make a rough model of some bilaterally symmetrical animal such as a fish, using modelling clay or some similar material. Practice making the various types of sections until you are completely familiar with these terms.

QUESTIONS

1. In what way does the analogy between the cells of the body and the bricks of a house break down?
2. What are the chief differences between plant and animal cells?
3. What is the function of the nucleus?
4. Why are chloroplasts important to the plant cell?
5. Which tissues of plants and animals are comparable?
6. Differentiate between the several types of muscle tissue.
7. What kinds of tissue make up the following: (*a*) the eyeball, (*b*) the lung, (*c*) the intestines, (*d*) the sweat glands, (*e*) the liver?
8. What is meant by anterior, ventral and medial?
9. What kind of body plan do the following organisms have: (*a*) starfish, (*b*) earthworm, (*c*) clam, (*d*) oak tree, (*e*) abalone?
10. List all the places in the human body where epithelial tissues are found.
11. How would you describe the position of the hump of a camel? Of a cat's eyes in relation to its nose?

SUPPLEMENTARY READINGS

DeRobertis, E. D. P., Nowinski, W. W., and Saez, F. A.: *General Cytology*. Philadelphia, W. B. Saunders Company, 1948.

A discussion of the properties of cells and cytoplasm, with a number of electron micrographs of tissues.

Maximow, A. A., and Bloom, W.: *A Textbook of Histology*. 5th ed. Philadelphia, W. B. Saunders Company, 1948.

A detailed classification and description of the tissues of the body; includes excellent pictures of each type.

PART II

THE VARIETY OF LIFE

CHAPTER 5

THE PLANT KINGDOM

THE WORD "plant" suggests trees, shrubs, flowers, grasses and vines—the large and familiar objects of our everyday world. Further thought brings to mind such forms as ferns, mosses and mushrooms, which are quite different, but recognizable as "plants." In addition, many unfamiliar, microscopic organisms—pond scums, molds and bacteria—are also plants. Some of these microscopic forms have characteristics in common with both plants and animals, so that it is difficult to determine whether they should be classified as plants or animals, or placed in a separate category of their own.

Fundamentally, plants and animals are alike in many ways, since both are made up of those small structural units, the cells, which, wherever they are found, carry on certain chemical processes vital to their existence. For these processes, resulting in growth and reproduction, the cells require food, water and oxygen. So much do plants and animals have in common, but there are many ways—some of them obvious, some rather obscure—in which the two main kinds of living organisms differ from each other.

To begin with the less important differences, plant cells, in general, secrete a hard, outer cell wall of cellulose, which encloses the living cell and supports the plant, while animal cells have no outer wall and hence can change their shape.

Secondly, plant growth is indeterminate; that is, plants keep on growing indefinitely because some of the cells remain in an actively growing state throughout life. Many of the tropical plants grow throughout the year; those in the temperate regions grow primarily in spring and summer. But although the cells of animals are replaced from time to time, the ultimate body size is established after a definite period of growth, and remains the same thereafter.

A third difference between the two types of living things is that most animals are able to move about, while most plants remain fixed in one spot, sending roots into the soil for various chemicals and obtaining energy from the sun through the exposure of broad, flat surfaces.

This brings us to the most important difference between the two: the ways in which they supply their cells with nourishment. Animals, being able to move about, obtain their food from the organisms of their environment; but plants, being stationary, must be more self-dependent. The outstanding thing, then, about plants in general is that they manufacture their own food from certain raw materials. This process, called **photosynthesis**, depends on a green pigment, **chlorophyll**, and is one of the most basic and important processes in the entire world of life.

1. Plant Nutrition. Plants which can synthesize their own food are said to be **autotrophic** (self-nourishing). Although the majority have this ability, there is one group of plants—the fungi—which do not.

TECHNOLOGICAL RE

These plants, which include the bacteria, are dependent, like animals, on their environment for food, and must live either at the expense of other organisms or upon decaying organic matter. Such plants are called **heterotrophic.**

There are several types of heterotrophic nutrition. When food is obtained as solid particles which must be eaten, digested and absorbed, after the fashion in which most animals obtain it, the process is called **holozoic** nutrition. A few of the insect-eating plants have a type of nutrition which is partly holozoic and partly autotrophic.

Another type of heterotrophic nutrition, in which food passes directly through the cell membrane, and which requires no digestive system, is called **saprophytic.** It is the type of nutrition carried on by most bacteria,* yeasts and molds. The environments favorable for this type of nutrition are limited, and saprophytes are usually confined to locations where there are decomposing bodies of animals or plants, or masses of animal and plant by-products. Yeasts are good examples of saprophytic plants. They need only inorganic salts, oxygen and some kind of sugar. From the last they can make all the other organic chemicals required—proteins, fats, vitamins, and so on. When there is plenty of oxygen available, the yeasts obtain energy by oxidizing the glucose completely to carbon dioxide and water. But in the absence of a sufficient amount of oxygen to do this, they ferment the glucose and form alcohol and carbon dioxide, using an enzyme known as zymase. The only practicable way in which ethyl alcohol can be obtained is through this action of yeast; hence yeast is used in the manufacture of all alcoholic beverages. It is also used in industries which manufacture alcohol for use as a solvent, or as a raw material for the production of other substances. Yeasts have a remarkable resistance to the toxic effects of alcohol, and continue forming the substance until a concentration of about 12 per cent is reached, at which point the action is inhibited. To produce beverages of higher alcoholic content, the wine or mash must be distilled. When yeast is mixed with bread dough, it ferments some of the sugar present; most of the alcohol produced is dissipated during the baking process, but the bubbles of carbon dioxide trapped in the dough expand and raise it, making the bread porous.

Another saprophyte, the red baker's mold, *Neurospora,* requires the vitamin biotin, in addition to salts and sugar; other saprophytes may require many different organic compounds.

A third type of heterotrophic nutrition, found among both plants and animals, is **parasitism.** A parasite lives in or on the living body of a plant or animal and obtains its nourishment from it. Almost every living organism is the host for one or more parasites. Some parasites do not harm the host, but others either deprive it of much of its nutritive materials, or injure its cells in some way and so produce disease. A few plants, such as the mistletoe, are partly parasitic and partly autotrophic, for although they have chlorophyll and make some of their food, their roots grow into the stems of other plants, and they absorb some of their nutrients from their hosts.

* A few of the bacteria are autotrophic, obtaining the energy necessary for the synthesis of food from the oxidation of certain inorganic chemicals in the soil or water (see p. 550).

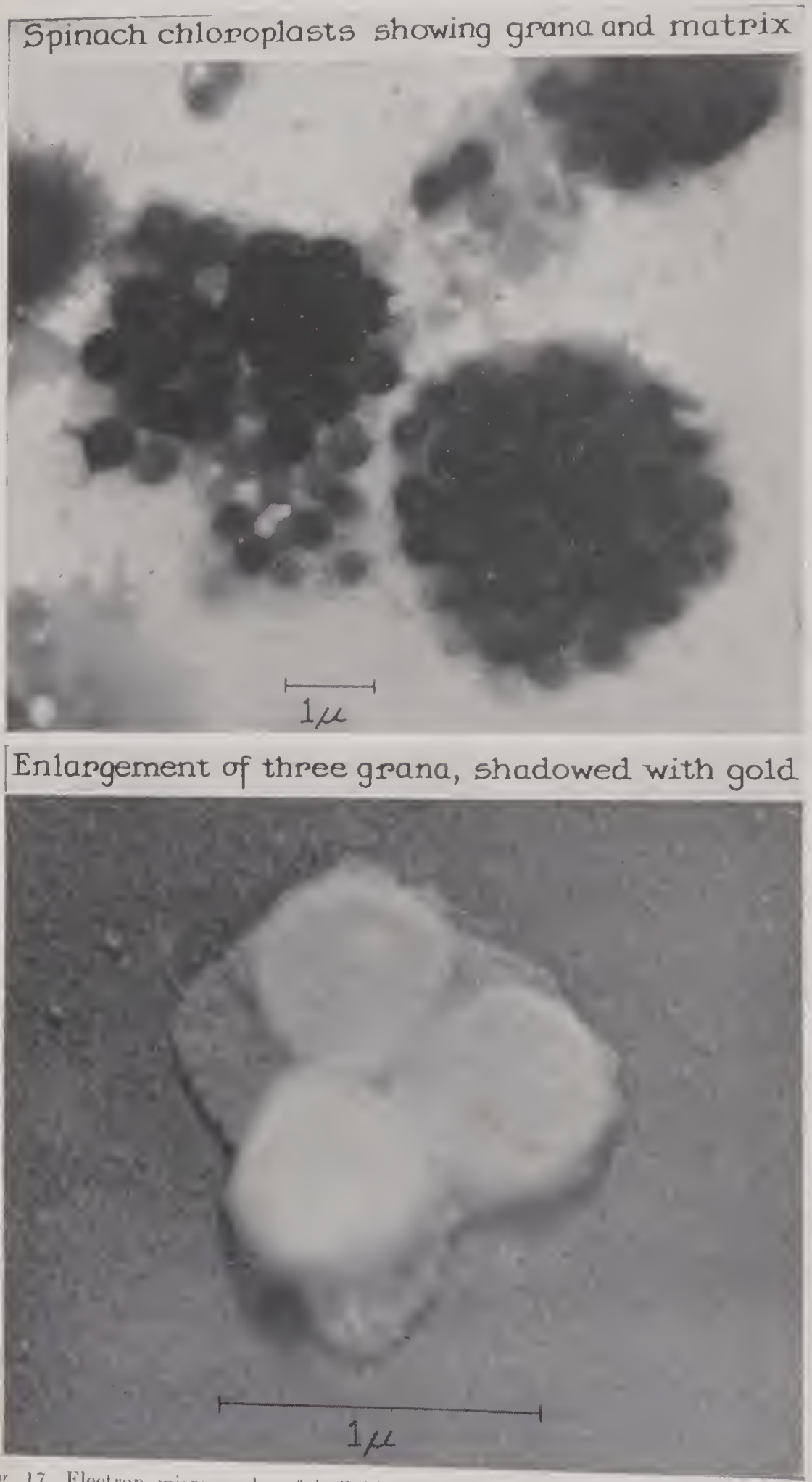


Fig. 17. Electron micrographs of individual chloroplasts from spinach leaves, showing the tiny, spherical bodies, called grana, within each chloroplast. (Courtesy of Dr. S. Granick, Rockefeller Institute for Medical Research.)

2. Photosynthesis. Photosynthesis is the process by which, in the presence of light, plants synthesize carbohydrates from water and carbon dioxide. The fact that carbohydrates, which are capable of releasing much energy, are made from two substances which have no physiological value as fuels, makes the process an interesting one. It is also noteworthy in being the only significant way in which the energy from the sun is captured and made available for life on this planet. Photosynthesis is not only the most important, but also the most widespread and frequent of all the chemical processes in nature. A tremendous amount of carbon (estimates place the actual amount at about 300 billion tons) is made into organic material each year by the green plants. Of this total, the land plants are responsible for about one tenth, the marine plants, mostly microscopic algae, manufacturing the rest. The general characteristics of photosynthesis are the same from the lowest plants to the highest, but there are minor variations in the photosynthetic mechanism in various plants.

The electron microscope has shown that the substance which enables plants to carry on photosynthesis—the green pigment, chlorophyll—exists within the plant cell in tiny bodies called **grana** (Fig. 17). These bodies, in turn, exist within larger bodies called **chloroplasts**, which are constantly growing larger and longer until they divide in the center to form two daughter chloroplasts. The over-all photosynthetic process occurs only in the green parts of the plants, where the grana are located. For example, in the leaves of variegated ivy, it occurs only in the green and not in the white parts of a single leaf. Roots, which ordinarily are not exposed to light and do not contain chlorophyll, nevertheless can develop chlorophyll if exposed to light, and so carry on photosynthesis.

Chlorophyll is a complicated organic substance composed of many atoms of carbon and nitrogen joined together in a complicated ring, with an atom of magnesium in the middle. It is strikingly like the red pigment, hemoglobin, of the blood cells, which has an almost identical ring, but an atom of iron instead of magnesium in the center. Both chlorophyll and red blood pigment are joined in their respective cells to protein molecules, and are physiologically active only in this form.

Plants contain many pigments other than chlorophyll, which give them their wonderful colors. Some of these may also absorb light energy, and transfer it to chlorophyll to be used in photosynthesis. Most plants have a deep orange pigment, carotene, which can be converted in the animal body to vitamin A, and a yellow pigment, xanthophyll. In 1947, evidence was discovered that the red pigments of red algae are more effective in photosynthesis than the chlorophyll those plants contain.

The chemical formula for the changes which occur in photosynthesis is as follows: 6 molecules of water + 6 molecules of carbon dioxide + light energy from the sun (made available by the chlorophyll) yield 1 molecule of glucose + 6 molecules of oxygen. To make 180 gm. of glucose requires 673 Calories of light energy. In this way, light energy, which is otherwise useless to living things, is transformed into potential chemical energy in the glucose molecule. The process is also extremely important in replenishing the supply of oxygen in the atmosphere. The function performed by chlorophyll in photosynthesis is to absorb the

radiant energy of sunlight and make it available to the reacting chemicals. Ordinarily, only about 3 per cent of the absorbed light energy is converted to chemical energy in photosynthesis. But with weak light and ample amounts of carbon dioxide, the amount of energy converted may reach 30 per cent. There is no decrease in the concentration of chlorophyll in the leaves after intense photosynthesis, indicating that the pigment is a true catalyst and is not used up in the process.

Land plants absorb the water necessary for photosynthesis through their roots; aquatic plants receive it by diffusion from the surrounding medium. The necessary amount of carbon dioxide diffuses into the plant by way of small holes (stomata) in the surface of the leaves. Since carbon dioxide is steadily used up in photosynthesis, its concentration within the cell is always slightly lower than that in the atmosphere, so that more is constantly diffusing in. And as oxygen is produced in the process, its concentration in the cell is increased and it tends to diffuse out. The glucose formed also tends to diffuse away from the site of formation to other regions of lower concentration.

Plants need vast quantities of air to carry on photosynthesis, for air contains only 0.03 per cent carbon dioxide. Thus, 10,000 cubic feet of air are needed to yield 3 cubic feet of carbon dioxide. Plants generally grow much better and faster in air with a higher carbon dioxide content, and some greenhouses are artificially maintained with an atmosphere containing from 1 to 5 per cent of it. There are many reasons for believing that in past geological ages the air contained much more carbon dioxide than it does at present, and that plants grew more rapidly. It is believed also that the phenomenal growth of the giant tree ferns of some 250,000,000 years ago, whose remains were converted into coal, was made possible by a high concentration of carbon dioxide in the atmosphere.

The actual chemical process involved in photosynthesis is complex, involving many different steps. Scientists have known since 1905 that the over-all photosynthetic process includes at least two steps, one of which can occur in the dark, and is therefore called the "dark reaction," and one of which can occur only in the light. The light reaction occurs first and produces certain unstable intermediate compounds: the dark reaction then follows and converts these intermediates into carbohydrate and oxygen. The dark reaction occurs much more slowly than the light one and limits the rate at which the whole reaction occurs. Since the light reaction produces many more molecules of unstable intermediates in a given amount of time than the dark reaction can convert to carbohydrates, many of them return to their original condition.

The light energy absorbed is used to decompose the water involved in photosynthesis. The utilization of the resulting hydrogen and oxygen can occur in the absence of light. By using isotopic tracers, investigators found that the oxygen released in the process is derived from the decomposition of the water, and that none comes from the carbon dioxide. The carbon of the glucose formed comes, of course, from the carbon dioxide. The oxygen of the glucose also comes from the carbon dioxide, and the hydrogen of the glucose comes from the water.

The first step, then, in photosynthesis, is the utilization of light energy to decompose water (H_2O) to oxygen and hydrogen. Just how this occurs is not known; the hydrogen undoubtedly is not released as a gas, but is taken up by other chemicals (called hydrogen acceptors) which pass it on in a bucket brigade fashion, so that eventually it is combined with the carbon dioxide. The exact nature of the first chemical compound resulting from the union of the hydrogen and carbon dioxide is unknown. At present it is believed to be something like acetic acid, but not that substance itself. This "acetic acid-like" substance is converted, via a long series of intermediate organic acids, into simple sugar (glucose), which is converted by enzymes into starch for storage. This is necessary because starch, unlike glucose or sucrose, is insoluble in water and will not diffuse away from the storage place. Or the intermediates may be converted directly, by other enzymes, into fats, proteins and other organic compounds. These conversion processes of plants are similar to those of animals.

Until recently, photosynthesis was thought to be the only chemical process in nature by which carbon dioxide is converted to organic substances. But in 1935 it was discovered that bacteria also, under certain conditions, can convert carbon dioxide into organic materials such as glucose; and shortly after that the same chemical process was demonstrated in animal tissues, such as the liver and kidney. It is now believed that the unique characteristic of photosynthesis is the coupling of the action of light with the decomposition of water and the production of gaseous oxygen.

So far, investigators have been able to make photosynthesis occur in the test tube only in the presence of complete living cells, and not with extracts of them, although it is possible to get certain steps of the photosynthetic mechanism to occur in the test tube extracts. For example, chloroplasts and even a solution of chlorophyll (plus its protein) will release oxygen from water when illuminated.

3. Plant Respiration. The process of respiration, which must occur in every living cell, is the same in all organisms, involving the taking in of oxygen, the giving off of carbon dioxide, and the releasing of energy from glucose and other foods in a form in which it can be used in cellular activity. The over-all chemical formula of respiration, then, is just the reverse of that of photosynthesis. The two processes are compared in the following table:

Photosynthesis	*Respiration*
Occurs in only those cells of green plants which contain chlorophyll	Occurs in all living cells
Raw materials are water and carbon dioxide	Raw materials are oxygen and organic substances such as glucose
Occurs only when light shines on the cell	Occurs continuously, night and day
Energy is stored by the process	Energy is released by the process
The process increases the weight of the plant	The process decreases the weight of the plant
Products are oxygen and organic materials	Products are carbon dioxide and water

When a plant is illuminated, photosynthesis occurs at a rate ten to thirty times as great as that of respiration, so that the latter process is masked completely. But in the dark, when no photosynthesis is occurring, a small rate of respiration can be measured in all plant cells. Oxygen is carried to the cells, and carbon dioxide is carried from them, by simple diffusion, and no special respiratory organs are present or needed.

4. Plant Digestion and Circulation. Plants need no digestive system, since their food is made within the cells, or absorbed directly through the cell membranes, and food is either used at once or transported to another part, such as the stem or root, where it is stored for later use. The few insect-eating plants, although they have no organized digestive system, do secrete digestive enzymes similar to those secreted by animals. The simpler plants, which consist of single cells or small groups of cells, have no transporting or circulatory system, and no need for one, since simple diffusion suffices to bring in the substances the plant requires: water, carbon dioxide and salts. The larger and more complex land plants have a simple transporting system composed of phloem and xylem cells (see p. 46), the former carrying dissolved food substances, the latter carrying water. Transportation of materials by these cells is much slower than the movement of substances by an animal's blood stream. Foods and minerals travel primarily by diffusion, and water rises in the xylem tubes because of the combined forces of transpiration and root pressure.

5. Plant Coordination. The activities of the various parts of a plant are much more autonomous than are those of the parts of an animal, and such coordination as does exist is achieved almost entirely by direct chemical and physical means, such as growth hormones, rather than by a nervous system. Plants have developed no specialized sense organs and no nervous system, but actively growing plants will respond to a stimulus by growing more rapidly on one side, and hence bending toward or away from it. Such responses are called **tropisms**, the most common of which are **phototropism**, the response to light (Fig. 18), and **geotropism**, the response to gravity (Fig. 19). These responses can occur only in those parts of the plant that are growing and elongating, but the stimulus for them may be received in some distant part of the organism. Thus, although plants have no sense organs or nerves, some cells are more sensitive to certain stimuli than are others, and stimuli can be transmitted from one part of the plant to another. The roots of plants are positively geotropic and grow downwards, whereas the stems are negatively geotropic and grow upwards. If a growing plant is spun on a disc for a day or more, so that centrifugal force replaces the force of gravity, the stem will grow toward the center of the disc and the roots will grow toward the periphery.

The growth of many plants is influenced by the relative length of day and night, certain periods of daylight bringing about the growth of leaves and stems, others bringing about flowering and seed formation. Cosmos plants, for example, can be induced to flower early in the summer instead of late by artificially shortening the daily exposure to sunlight (Fig. 20). There is considerable evidence to show that the induc-

Fig. 18. Phototropism in young radish plants. *A*, In the dark or in uniform light, the plants grow straight upward. *B*, When they are exposed to light coming from a single direction, they quickly bend toward it—that is, they are positively phototropic. The photograph on the right was taken half an hour after the one on the left. (Weatherwax: Plant Biology.)

Fig. 19. Geotropism in young radish plants. *A*, Pot of straight radish seedlings placed on its side and kept in the dark to eliminate phototropism. *B*, Within thirty minutes the seedlings had bent; since they bend away from the direction of the force of gravity, they are negatively geotropic. (Weatherwax: Plant Biology.)

Fig. 20. Two cosmos plants grown in Washington, D. C., from seeds planted May 26. Normally, the plant begins to flower in late August or September, but by artificially shortening the exposure to light to ten hours a day, the plant on the left was induced to flower July 8. The plants which were exposed to the normal fourteen or fifteen hours of daylight per day are shown to the right. This response to the relative length of day and night is known as photoperiodism. (Weatherwax: Plant Biology; photograph courtesy of Dr. H. A. Allard and the United States Department of Agriculture.)

tion of flowering is regulated by a hormone, but the mechanism whereby this hormone is elicited by shortening or lengthening the daily exposures to light is unknown.

6. Plant Excretion. The metabolism of plants is such that scarcely any metabolic wastes are produced, and some of these are used over again in other metabolic processes. For this reason there is little for plants to excrete, and no special excretory system is needed. The main wastes of respiration, carbon dioxide and water, are used as raw materials in photosynthesis. A few plant cells accumulate special types of waste products, but instead of excreting them to the outside in some way, they usually deposit them as insoluble crystals, either in the cytoplasm itself or in the vacuoles.*

I. TYPES OF PLANTS

Although all green plants are similar in their basic chemical processes, there is among them a remarkable variety of size, shape, and degree of specialization. In the past the various kinds of plants were classified on the basis of whether they were trees, shrubs or herbs; or according to whether they produced fruit, vegetables, fibers or wood; or on the basis of structural similarities. With the acceptance of the theory of evolution, botanists tried to set up a system of classification based on natural relationships, putting in a single group those plants which are closely related in their origin. There are still disagreements, however, as to how certain groups should be classified, because not enough is known about their evolutionary history.

At the present time the unit of classification for both plants and animals is the **species.** It is difficult to give a definition of this term which will apply uniformly throughout the animal and plant kingdoms, but a species may be defined as a group of similar individuals, alike in their structural and functional characteristics, which breed only with each other, and have a common ancestry.

Closely related species are grouped together in the next higher unit of classification, the **genus** (plural, *genera*). The scientific names of plants and animals consist of two words, the genus and the species, given in Latin. This system of naming organisms, called the binomial (two-name) system, was devised about two hundred years ago by the Swedish naturalist Linnaeus. In accordance with it the scientific name of the domestic cat, *Felis domestica,* applies to all the varieties of tame cats—Persian, Siamese, Manx, Abyssinian and plain tabby—since they all belong to the same species. Related species of the same genus are *Felis leo,* the lion, *Felis tigris,* the tiger, and *Felis pardus,* the leopard. The dog, which belongs to a different genus, is named *Canis familiaris.* The use of Latin, rather than a modern language, in naming species is a carry-over from the days when Latin was the language of science. It is still used because it is widely understood and not subject to change as the "living" languages are.

* The modes of reproduction in the plant kingdom, as well as the life cycles of plants, are fully discussed in Chapter 16. The material covered there is of the utmost importance for understanding how plants live and how they differ from each other and from animals. It should be read in connection with this chapter.

Just as several species may be grouped together to form a genus, a number of related genera constitute a **family;** and families may be grouped into **orders,** orders into **classes,** and classes into **phyla** (singular, *phylum*). The phyla, then, are the large, main divisions of the plant and animal kingdoms, as the species are the fundamental, small units. The white oak is classified as phylum Spermatophyta, class Angiospermae, subclass Dictotyledoneae, order Sapindales, family Fagaceae, genus *Quercus,* species *alba.* Man belongs to the phylum Chordata, subphylum Vertebrata, class Mammalia, subclass Eutheria, order Primates, family Hominideae, genus *Homo,* species *sapiens.*

Many plants and animals fall into easily recognizable, natural groups, and their classification presents no difficulty, but other forms, which seem to lie on the borderline between two groups and have some characteristics in common with each, are difficult to assign to one or the

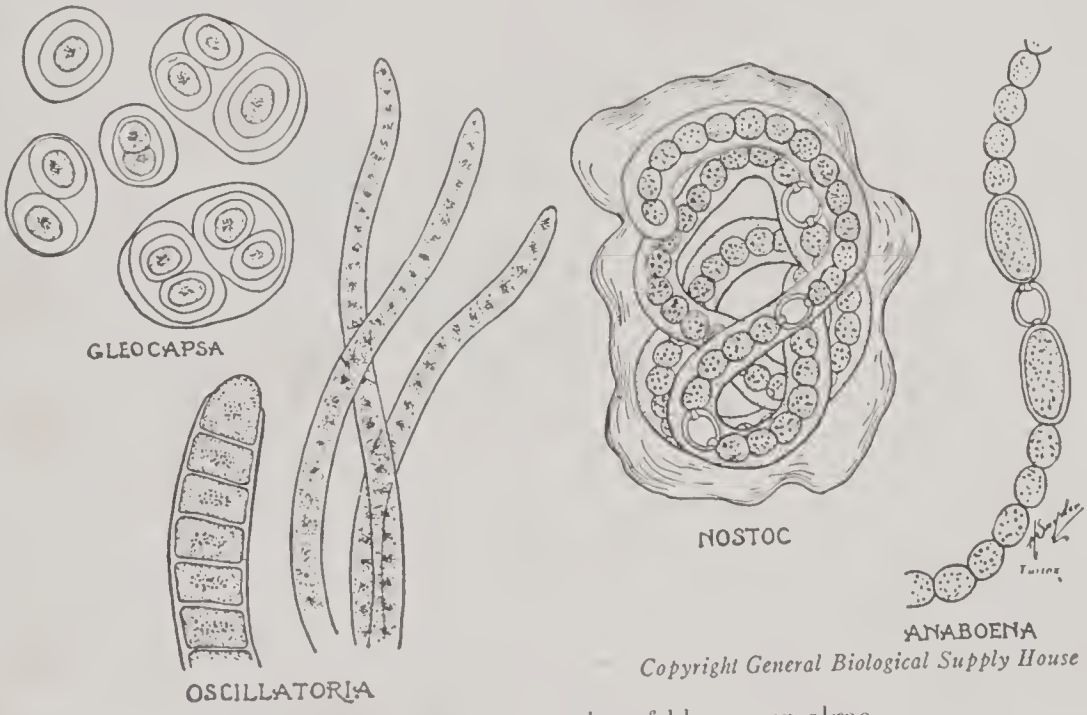


Fig. 21. Some common species of blue-green algae.

other. Because of this, the number and inclusiveness of the principal groups vary according to the basis of classification used, and the judgment of the scientist making the classification. Some taxonomists like to group things together in already existing units; others prefer to establish separate categories for forms that do not fall naturally into one of the recognized classifications. Thus different taxonomists consider that there are from ten to twenty-three phyla of animals, and from four to seven phyla of plants. We shall use the simpler method, and consider that there are four plant phyla, named, in order of increasing complexity, the Thallophyta, Bryophyta, Pteridophyta, and Spermatophyta.

7. Thallophyta. Among the 107,000 or so species which make up the phylum Thallophyta are the most primitive and simply organized plants. The phylum is made up of two subphyla, the **algae,** which have chlorophyll and can live independently, and the **fungi,** which lack chlorophyll and so must secure their food from organic material. The members of both subphyla are alike in having a body, called a **thallus,** which lacks

roots, stems or leaves. The thallus may be a single cell or an aggregate of many cells, but even in the latter case there is no differentiation into tissues.

Algae. Nearly all algae are aquatic, or practically so, for since they have no roots with which to secure moisture from the soil, they can live only immersed in water, or covered by a watery film. A few, however, grow in comparatively dry places such as the trunks of trees, and

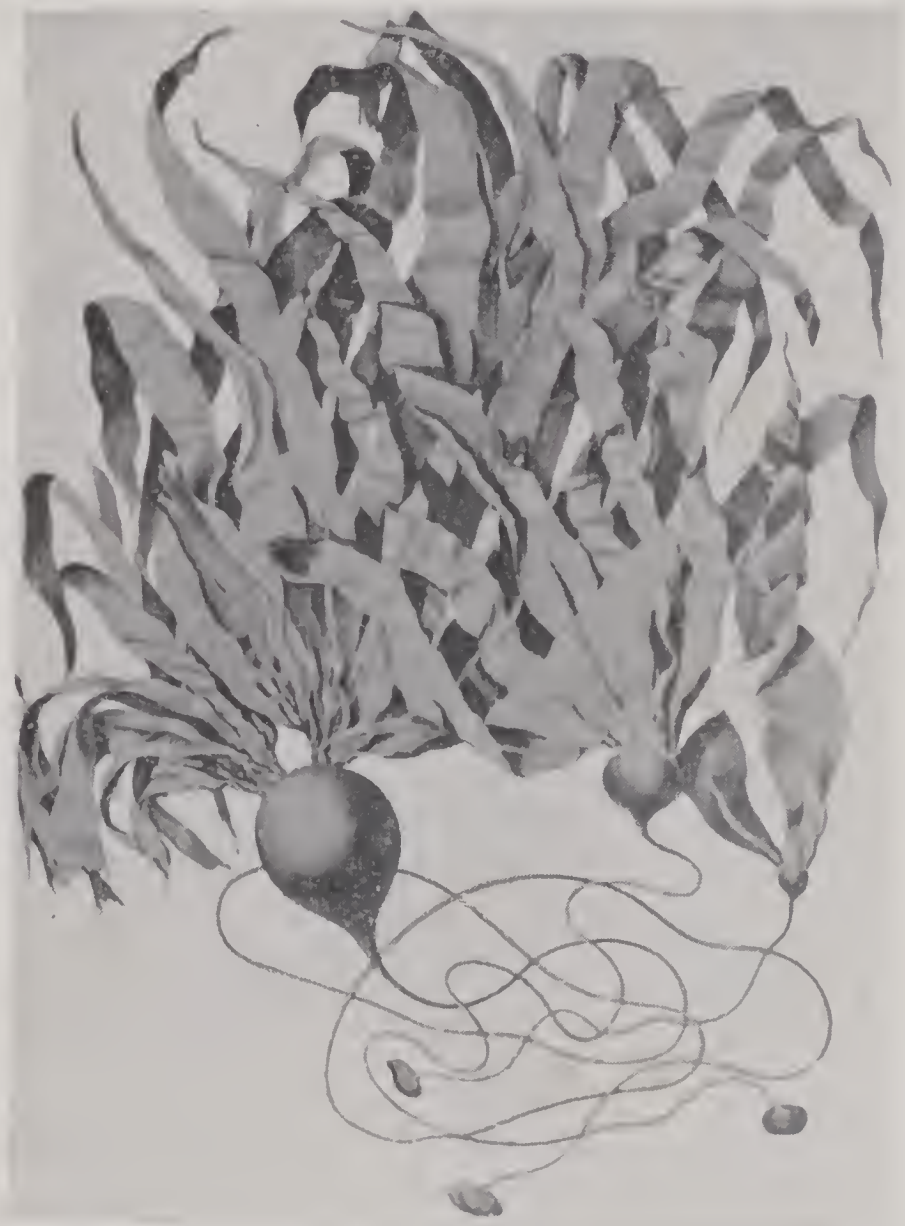


Fig. 22. Three small plants of the common brown alga or kelp, *Nereocystis*. Note the "holdfasts" by which the kelp is attached to the rock, and the turnip-shaped air bladders at the base of the leaflike, expanded portions of the thallus, which enable the plant to float. (Holman and Robbins: Textbook of General Botany, John Wiley & Sons, Inc.)

have developed the ability to remain dormant when water is absent and to metabolize and grow only during rainy spells. The algae may be unicellular or may have a branching, many-celled thallus, which superficially resembles the higher plants, but even the most complex thallophytes are much simpler in internal structure than any higher plant.

The algae form a diverse group which, since the plants have other pigments than chlorophyll, is subdivided on the basis of color. The blue or olive-green algae (Cyanophyceae) are the simplest algae and probably the most primitive of all existing plants. They float about in either

fresh or salt water, or live as scum on the surface of rocks in stagnant ponds (Fig. 21). Unicellular in structure, they are sometimes organized into loose filaments or colonies, but there is no distinct nucleus within the individual cell and no chloroplast. Reproduction occurs by simple cell division or by sporulation, never sexually.

The green or yellow-green algae (Chlorophyceae) live in either fresh or salt water, or in moist places on rocks or tree trunks. Sometimes they exist as single cells, sometimes in colonies or long filaments, and the individual cells may contain one or many nuclei and many chloroplasts.

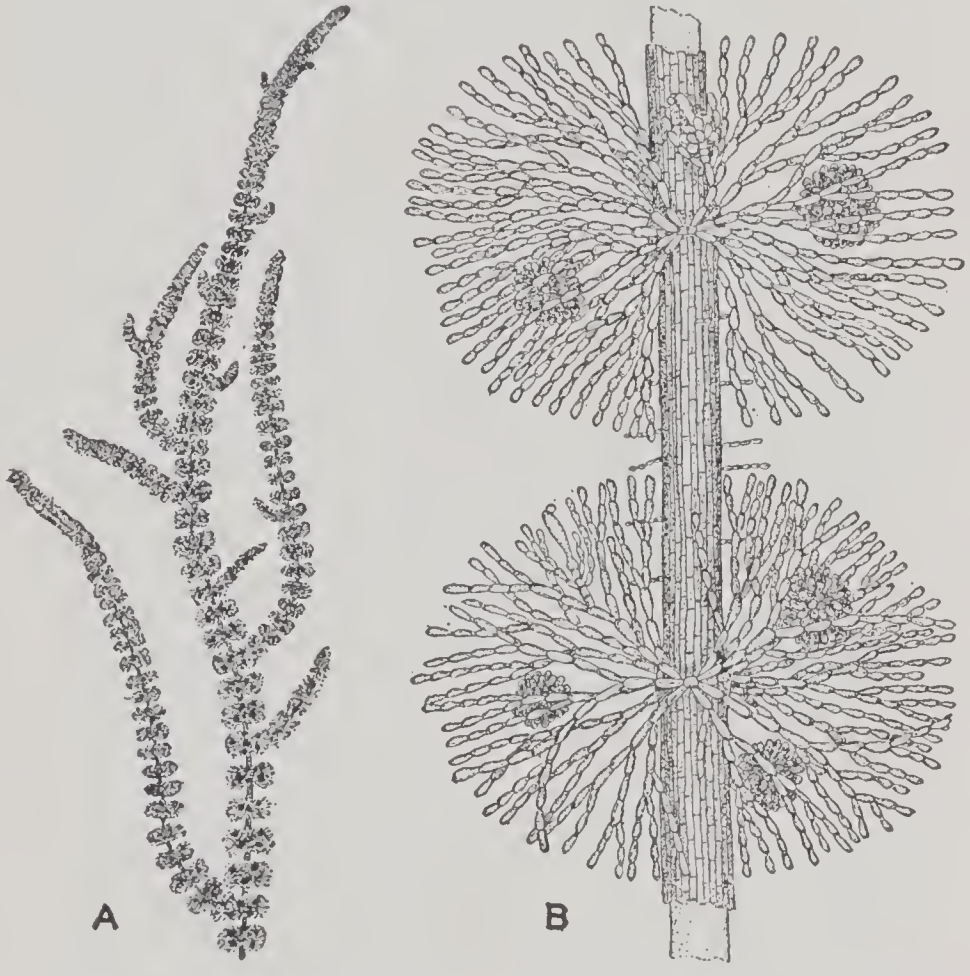


Fig. 23. *A*, Fresh-water red alga, *Batrachospermum*. *B*, Enlarged view of a part of its main stem, showing the whorls of small branches. (Weatherwax: Plant Biology.)

Reproduction may be sexual or asexual. *Acetabularia*, the umbrella-shaped marine alga described in Chapter 3, is a green alga, as are *Spirogyra*, *Ulothrix* and *Oedogonium*, whose methods of reproduction are described in Chapter 19.

The brown algae (Phaeophyceae) include the kelps and other brown seaweeds, and are found only in salt water, where they are attached by hold-fasts to rocks beneath the surface of the water, and buoyed up at the free ends by air bladders (Fig. 22). Some of these tough and leathery plants grow to a length of 500 feet. Reproduction is usually sexual, although some species show an alternation of sexual and asexual generations.

The red or purplish algae (Rhodophyceae) are the red sea weeds, most of which live in salt water, although there are a few fresh-water

forms. Their bodies are frequently delicately branched (Fig. 23), and some of them have walls hardened with calcium carbonate which contribute to the formation of coral reefs.

The various types of algae are important biologically as a source of food and oxygen for many aquatic animals, and the larger ones also provide a place of attachment and of hiding for a great variety of marine creatures.

Fungi. There are many more types of fungi than algae, and the fungi include plants that are diverse in their structure and way of living. Some fungi are saprophytic, others parasitic.

The bacteria (Schizomycetes) are unicellular fungi that live in a wide variety of habitats, and are parasitic or saprophytic. Their cells are simple, and they resemble the blue-green algae except for their lack of chlorophyll. Reproduction takes place by simple cell division or by sporulation.

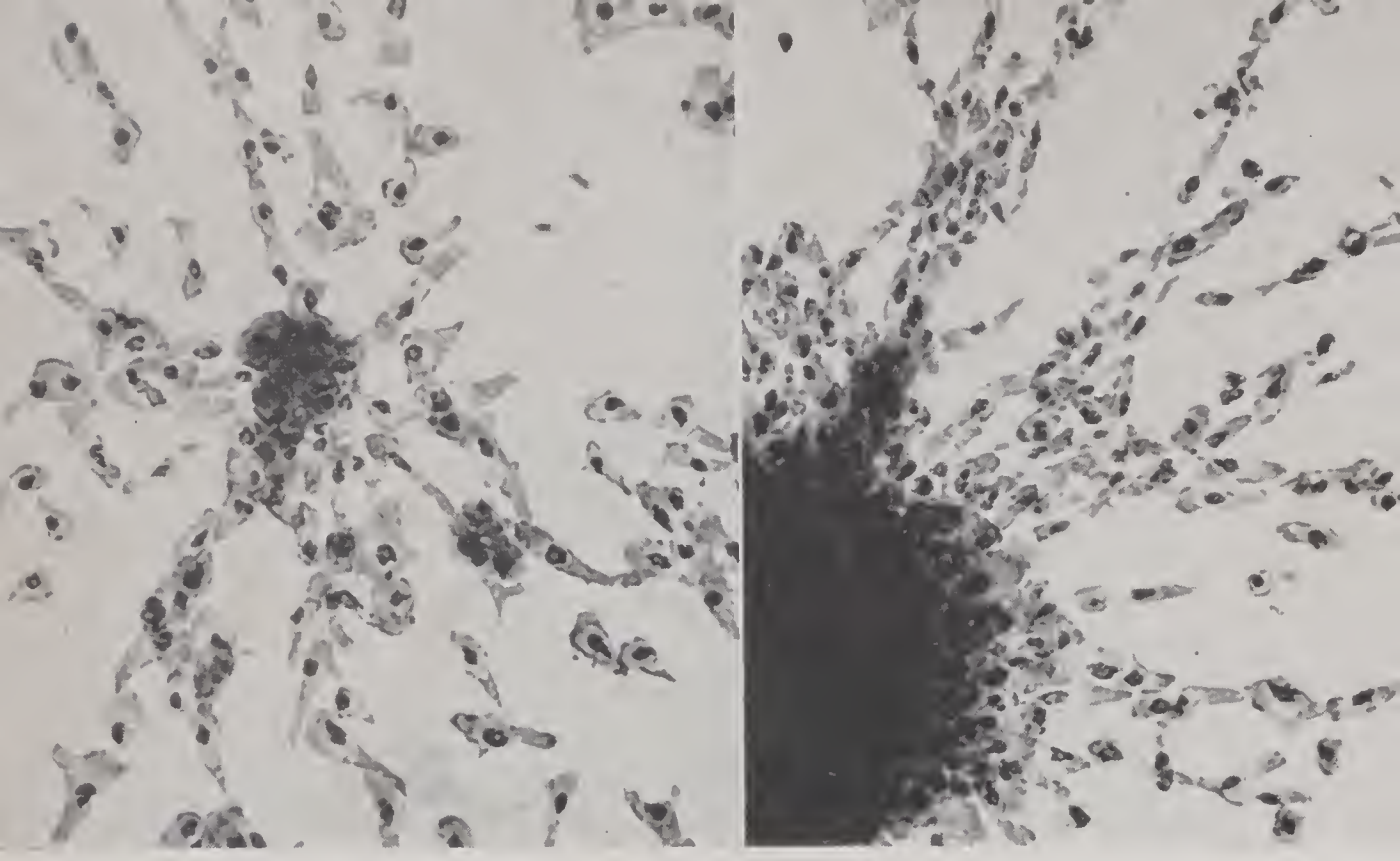
The slime molds (Myxomycetes) are peculiar organisms which resemble other fungi in some respects, but, during part of their lives, are very like amebas. They exist as slimy masses on decaying leaves, and move by sending out pseudopodia, just as amebas do. Although each mass contains many nuclei, it is not divided into individual cells. Ordinarily, these plants reproduce by fission, but one of the most curious of biological phenomena is the way in which, at certain times, individual slime molds congregate to form a fruiting (spore-producing) body (Fig. 24), thus making an alternate type of reproduction possible.

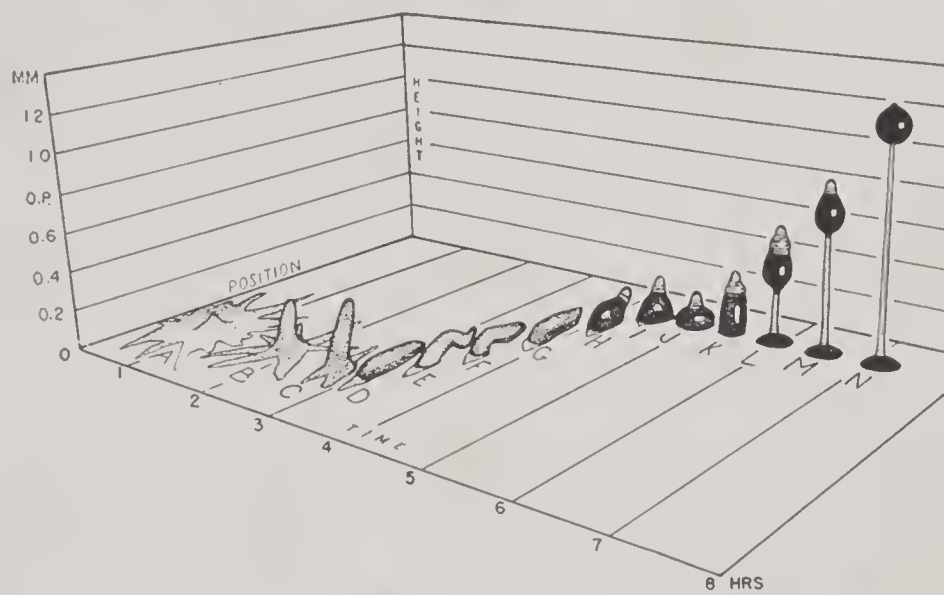
The Phycomycetes, or algal fungi, take their name from the fact that in their body form, which consists of long filaments, and in their method of reproduction by means of motile spores, or sexually by means of gametes, they resemble algae. The body, or hypha, of these plants is a long, unicellular tube with many nuclei. Some species, such as the bread mold (Fig. 25), cause decay; others, such as the downy mildews, cause plant diseases.

The largest class of fungi, the sac fungi (Ascomycetes), are so called because their spores are produced in sacs, called asci (singular, *ascus*). The class includes yeasts, powdery mildews, the molds which appear on cheese, jelly and fruit, and the truffle, which is regarded as a delicacy in Europe. The ascomycete molds which appear on food may give it an unpleasant taste, but they are not poisonous and may be eaten safely. In fact, they are essential for the flavor of cheeses such as Roquefort and Camembert. The antibiotic penicillin is produced by an ascomycete, *Penicillium*. The bodies of ascomycetes consist of threadlike branches, called hyphae, with the nuclei separated from one another by cross walls. Reproduction is accomplished asexually by spores, or sexually by gametes which unite to form a "fruit,"* containing the ascus.

The Basidiomycetes is a class of fungi which includes the mushroom and toadstool, as well as the puff ball, the rusts and smut of wheat, and the bracket fungus. The name indicates that all the members of the class have **basidia**, special cells with four slender branches, which produce spores (basidiospores) at their tips. Sometimes one, sometimes

* The structures in which asci are produced are often large and fleshy, superficially resembling true fruits, but bearing no relation to them.





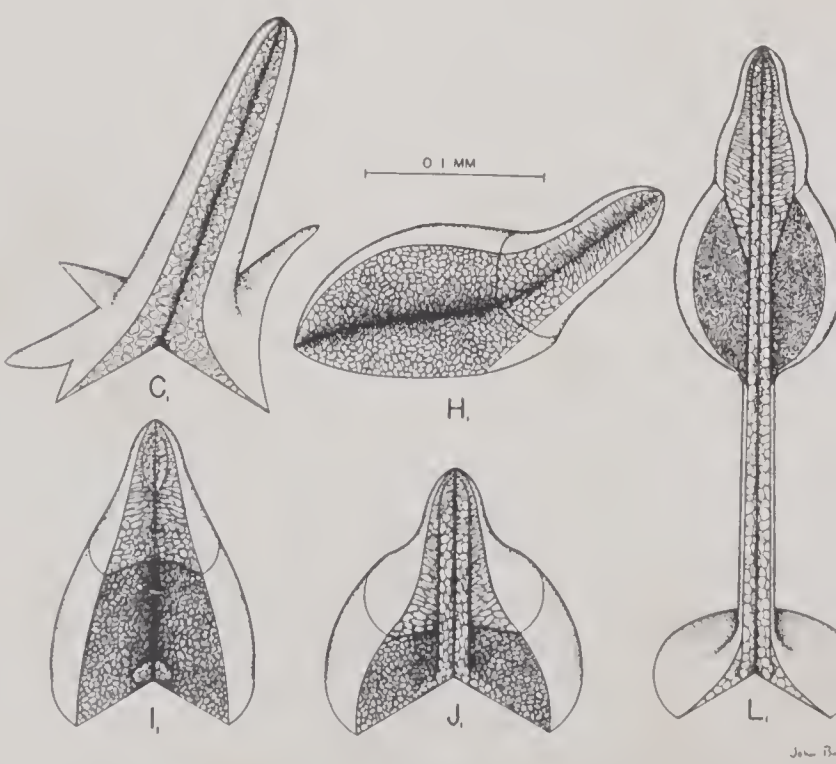


Fig. 24. Reproduction in slime molds. *Upper left*, Photomicrograph showing individual organisms beginning to congregate as a fruiting body. *Upper right*, Photomicrograph showing a later stage in the process of congregation. *Below*, Diagram of the various stages in the process. *A–C*, the fruiting body is formed by the aggregation of hundreds of individual ameba-like slime molds; *D–H*, it crawls along the substrate surface for some time; *I–N*, it grows a stalk which lifts the spore-producing part off the surface. Finally, the spores are released. (Courtesy of Dr. John Bonner.)

countless basidia exist in a single plant. The bodies of these fungi are multicellular structures with the fleshy, spore-bearing part supported by a network of filaments in the soil. The underside of a mushroom or toadstool umbrella is made of filaments arranged in various patterns, and bearing club-shaped basidia at their tips (Fig. 26). When the basidiospores are mature, they are released in great numbers and carried by the wind to new places of development.

After the easily classifiable fungi have been assigned to one of the foregoing five classes, there are some left over that do not seem to fit in anywhere. These are lumped together in a heterogeneous group, known as the **imperfect fungi,** not because they are imperfectly formed, but

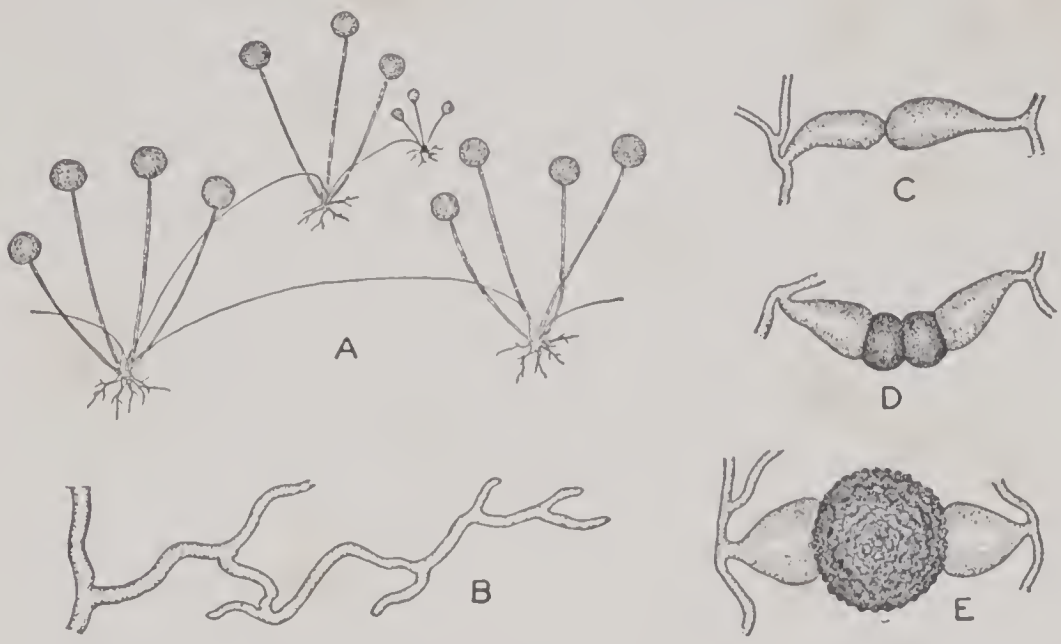


Fig. 25. *A*, Bread mold magnified ten times; the spherical structures are sporangia, in which develop spores for asexual reproduction. *B*, Enlarged view of a mycelium—the fine, white, rootlike filaments which grow down inside the bread. *C–E*, Stages in the sexual reproduction of the bread mold by fusion of two branches to form a zygote. (Weatherwax: Plant Biology.)

because their status is imperfectly understood. Sexual reproduction is unknown in this group; for some, this is due to a true loss of the fruiting phase, so that only asexual spores are produced; for others, there very likely is a fruiting phase which has not been identified as yet. The imperfect fungi include some forms which cause important plant diseases, such as leafspot.

The **lichens** are curious plants which, although they look like individual plants, are really an intimate combination of an alga and a fungus (Fig. 27). The algal component is either a green or a blue-green alga, and the fungus is usually an ascomycete, although it may be a basidiomycete. A lichen, then is really a fungus body with algal cells imbedded in it. Lichens are resistant to extremes of temperature and moisture, and grow everywhere that life can be supported at all. They exist farther north than any other plants of the arctic region, and are equally at home in the steaming equatorial jungle. The alga, by photosynthesis, produces food for both plants, while the fungus protects the alga and provides it with moisture and mineral salts.

The fungi are important biologically as scavengers which consume dead organic material and make it available for re-use (p. 386). But they are also responsible for devastating economic losses, by causing both disease and the decay of food, clothing, wood and other materials.

8. The Conquest of Land by Plants. Since all green plants require water, salts, carbon dioxide and light, the process whereby land plants developed from the first primitive, aquatic algae must have been a long and complicated one, fraught with many failures. For the new forms which tried to live in the soil there were plenty of salts, water and carbon dioxide, but no light, and for those which tried to live above ground there was sufficient light and carbon dioxide, but not enough water and no salts. The plants which finally triumphed and were able to exist on land did so by means of specialized parts: **leaves,** which extended into the air to absorb light and carry on photosynthesis; **roots,** which extended into the soil to absorb water and salts, and to act as

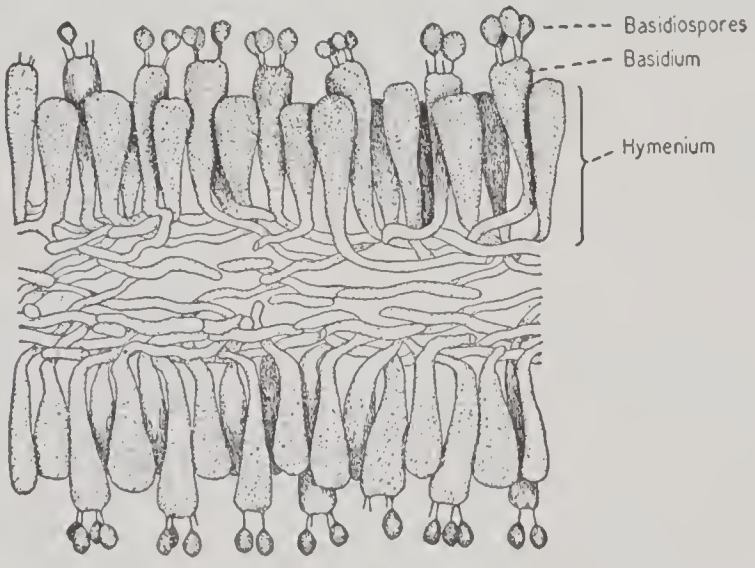


Fig. 26. Section of a gill from the under side of a mushroom cap, magnified 500 times, to show the basidia and their basidospores. (Weatherwax: Plant Biology.)

anchors for the plants; and **stems,** which connected the two and provided a passage way for vital substances.

9. Bryophyta. The simplest and most primitive plants with stems, roots and leaves are the **bryophytes**—the mosses and liverworts. Their advance over the algae is simply in having differentiated cells, specialized for particular functions, which make possible a division of labor. The name "moss" is frequently applied to plants which are not true bryophytes at all, such as the "moss" on the north or shady side of tree trunks, which is really an alga. Both lichens and liverworts are commonly mistaken for mosses. The "Spanish moss" found on trees in the South is really a seed plant, related to the pineapple.

There are some 23,000 species of mosses and liverworts, found in all climates and habitats; some species are able to live only in damp places, others can live on dry sand or rocks where enough moisture for growth is present only a short part of the year.

The **mosses** are all rather similar in structure, consisting of a single stem, or axis, to which are attached a great number of leaves (Fig. 156).

From the base of the stem many rootlike projections, called **rhizoids,** extend into the ground. Mosses never exceed 6 or 7 inches in height, owing to the inefficiency of the rhizoids as water absorbers. The stems, too, because of their fragility and lack of a true vascular system for

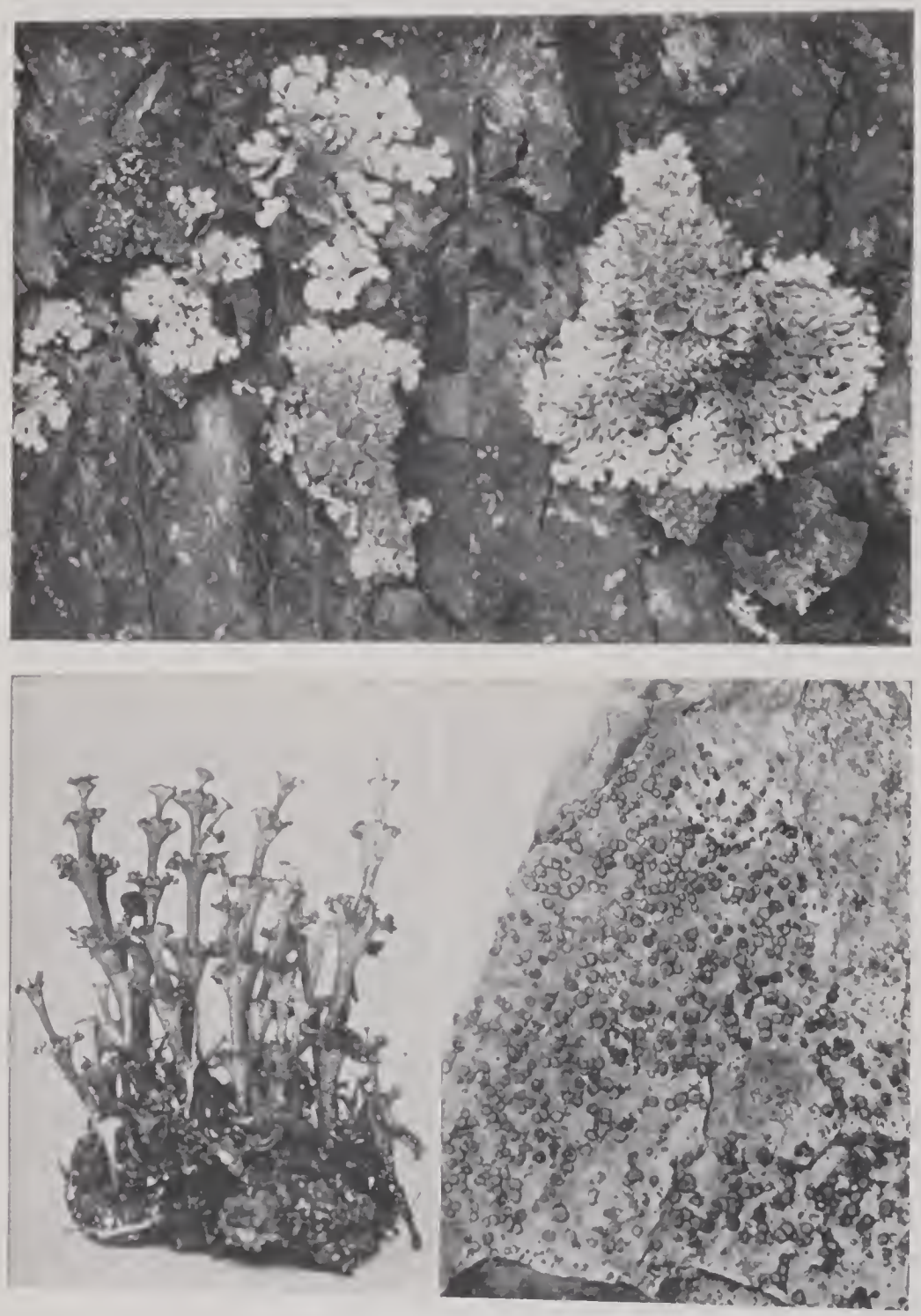


Fig. 27. Types of lichens. *Above,* Leafy type growing on the bark of a tree. *Lower left,* The lichen known as "reindeer moss." *Lower right,* An encrusting type growing on the surface of a rock. On each type can be seen some cup-shaped fruiting bodies. (Weatherwax: Plant Biology.)

moving water and food over long distances, would be incapable of supporting larger bodies. For protection from excessive loss of water by evaporation, most bryophytes have developed a specialized outer layer of cells, the **epidermis,** which secretes, as does the epidermis of higher plants, a layer of thin, waterproof material called **cutin.** But beneficial

and necessary as the epidermis is, it interferes with the movement of gases involved in photosynthesis and respiration, a difficulty overcome by small holes in the epidermis known as **stomata** (singular, *stoma*).

Both mosses and liverworts show a marked alternation of sexual and asexual generations (see p. 339). The conspicuous, familiar plant is the sexual or gametophyte generation; the sporophyte or asexual generation develops as a parasite on the top of the female gametophyte. Mosses are successful in spreading over large areas partly because of the facility with which they can propagate asexually by means of underground runners.

An economically important moss is *Sphagnum*, which grows in bogs in North America and Europe and is one of the main constituents of peat, used for fuel in many countries.

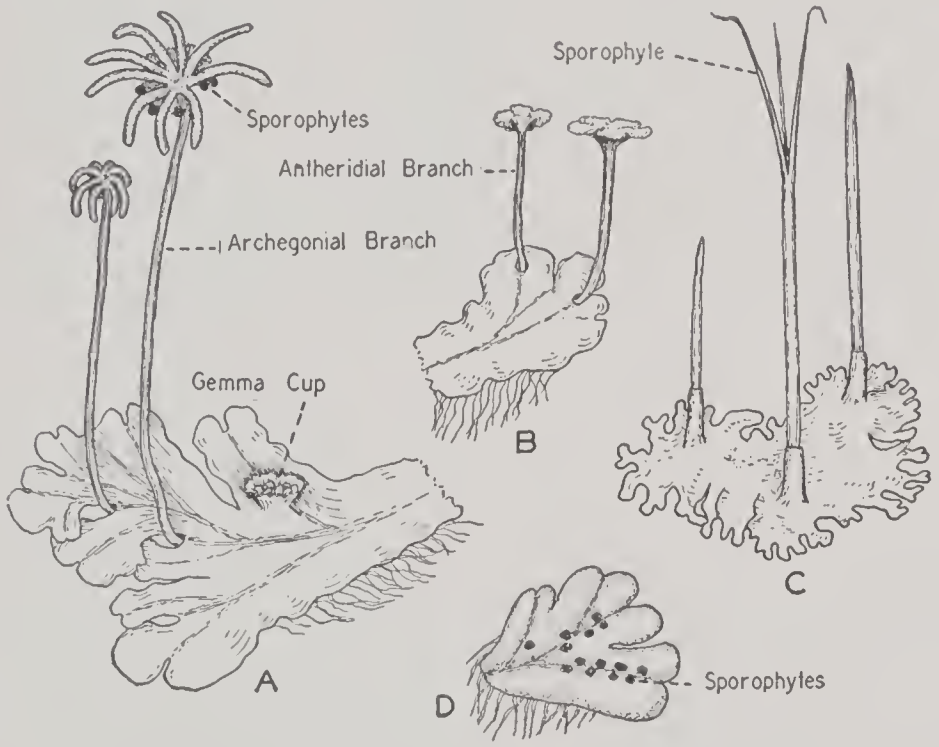


Fig. 28. Sketches of some common liverworts. *A* and *B Marchantia* (natural size); *C*, *Anthoceras*, and *D. Riccia* (magnified three times). In each, the main, flat part of the body is the gametophyte, from which the sporophyte develops. (Weatherwax: Plant Biology.)

Liverworts, the other class of bryophytes, are simpler and more primitive than the mosses. Their bodies consist of a flat, sometimes branched, leaflike structure that lies on the ground, in contrast to the upright position of the mosses. This body, usually no more than an inch or two in diameter, is attached to the soil by numerous rhizoids, and lacks a stem. The epidermis of the upper surface is covered with waxy cutin to prevent the loss of water, and is punctured by many stomata for the exchange of gases. The recognizable plant is the gametophyte generation; as in mosses, the sporophyte grows as a parasite on the gametophyte (Fig. 28).

Mosses and liverworts evolved from alga-like ancestors, and certain green algae have many characteristics in common with the simpler liverworts. The mosses, apparently, represent the end of one branch of the

evolutionary tree; that is, they are not believed to have given rise to any higher plants. Instead, the higher plants are generally considered to have come either from liverwort-like plants or directly from the algae.

10. Pteridophyta. This phylum includes some diverse types of plants: the ferns, the ground pines or club mosses, and the horsetails (and their fossil relatives). In addition, there were once many thousands of other species, now known only from their fossil remains. The evolutionary relationships of these four classes are rather obscure, and the ferns may actually be more closely related to the higher, seed plants than to the other members of the Pteridophyta. But diverse as the various classes seem, they have, of course, a number of characteristics in common. They differ fundamentally from the thallophytes and bryophytes in having a much more complex sporophyte plant. They also have well-developed leaves, stems and roots, and a true vascular system. In this they resemble the spermatophytes (seed plants), with which they are sometimes grouped under the name, "vascular plants." They are unlike the spermatophytes in that they do not produce seeds, although this is probably not so basic a difference as was once believed, for fossil plants have been found with the general characteristics of pteridophytes, which did produce seeds. In contrast to the bryophytes, in which the gametophyte is the important generation and the sporophyte parasitic upon it, the pteridophyte sporophyte is the important, independent plant, and the gametophyte, although capable of independent existence, is a small, structurally simple plant that is hardly recognizable as a fern (Fig. 157).

The important advances of the ferns over the mosses are the evolution of the conducting tissues, which carry water and food from one part of the body to another, and permit the plants to grow to a large size, and the concomitant evolution of woody, or fibrous, supporting tissues. The fossil tree ferns often towered to a height of 100 feet, and although present-day temperate zone ferns are small, the modern tropical tree ferns average around 30 feet and do achieve, though rarely, a height of 70 feet. The latter superficially resemble palm trees, having an erect, woody, unbranched stem with a cluster of fronds (compound leaves) at the top; actually, they are unrelated to them.

There are about 9000 species of pteridophytes living today, 8000 of which are ferns; the rest are horsetails, club mosses and quillworts. Ferns are common, widespread plants, growing best in moist, shady places, but some, such as the bracken fern, can live in dry environments. The common, temperate-zone ferns usually have a horizontal, underground stem, from which arise the fronds. The leaves of ferns characteristically are coiled in the bud and unroll and expand to form the mature leaf.

Horsetails are widespread plants, too, usually less than 15 inches tall, occurring from the tropics to the Arctic, on all continents except Australia, and in both boggy and dry places. The name "horsetail" comes from the multiple-branched, bushy structure of many species. Another popular name, "scouring rushes," is based on the fact that deposits of sand and silica in the epidermis give the plants a harsh, abrasive quality. In this capacity they were used for centuries before the invention of steel wool. The sporophyte plant is made up of many branching roots,

from which branch jointed, aerial stems and subterranean roots (Fig. 29). Since the leaves are small and rudimentary, most of the photosynthesis occurs in the stem. Some of the stem tips develop spore-bearing leaves, analagous to those of the true ferns.

Fig. 29. Sketch, half natural size, of a horsetail, *Equisetum,* one kind of pteridophyte. Inset, natural size, the cones of this plant. (Weatherwax: Plant Biology.)

The **club mosses** or **ground pines** are widespread but inconspicuous plants, consisting of a creeping stem which gives off upright stems with conelike, spore-bearing structures at their tips (Fig. 30), and thin, flat, spirally arranged leaves.

The **quillworts,** which belong to the same class as the club mosses, are superficially quite different from the other pteridophytes, with slen-

der, quill-like leaves resembling those of a bunch of garlic (Fig. 31). The leaves are attached by their broad bases to a short stem, out of which the roots grow. The leaves have spore-bearing organs at the basal end.

11. Spermatophyta. The spermatophytes, or seed plants, are the most highly developed and widespread phylum of plants. The 150,000 or so species which make up the group primarily have in common the method of reproduction by **seeds** (see p. 343), but vary so strikingly in size, shape and other characteristics that it is questionable whether they constitute a single, natural group which arose from a single, common

Fig. 30. *A*, Photograph, half natural size, of a club moss, *Lycopodium*, another kind of pteridophyte. *B*, Enlarged view of a single stem, showing the arrangement of the leaves. (Weatherwax: Plant Biology.)

ancestor. Another important characteristic is the formation of **pollen tubes.** These organs transfer the sperm of seed plants directly to the egg, so that, in contrast to the lower plants, fertilization is not dependent on the presence of water, and the seed plants can reproduce in a wide variety of environments. This has contributed greatly to their becoming the dominant land plants.

The phylum Spermatophyta includes the plants most familiar and economically important to man—trees, shrubs, vines, grasses and flowering plants. The two classes of the phylum are the **gymnosperms** (naked seeds) and the **angiosperms** (enclosed seeds), which differ in the relationship of the seeds to the structures producing them. The seeds of angiosperms are formed inside a fruit, and the seed covering is developed

from one or more carpels (see p. 342) of the flower.* The seeds of the gymnosperms are borne in various ways, usually on cones, but they are never really enclosed as are angiosperm seeds. Seeds have contributed to the success of the spermatophytes: their store of food nourishes the embryo until it can lead an independent life; their tough, outer coat pro-

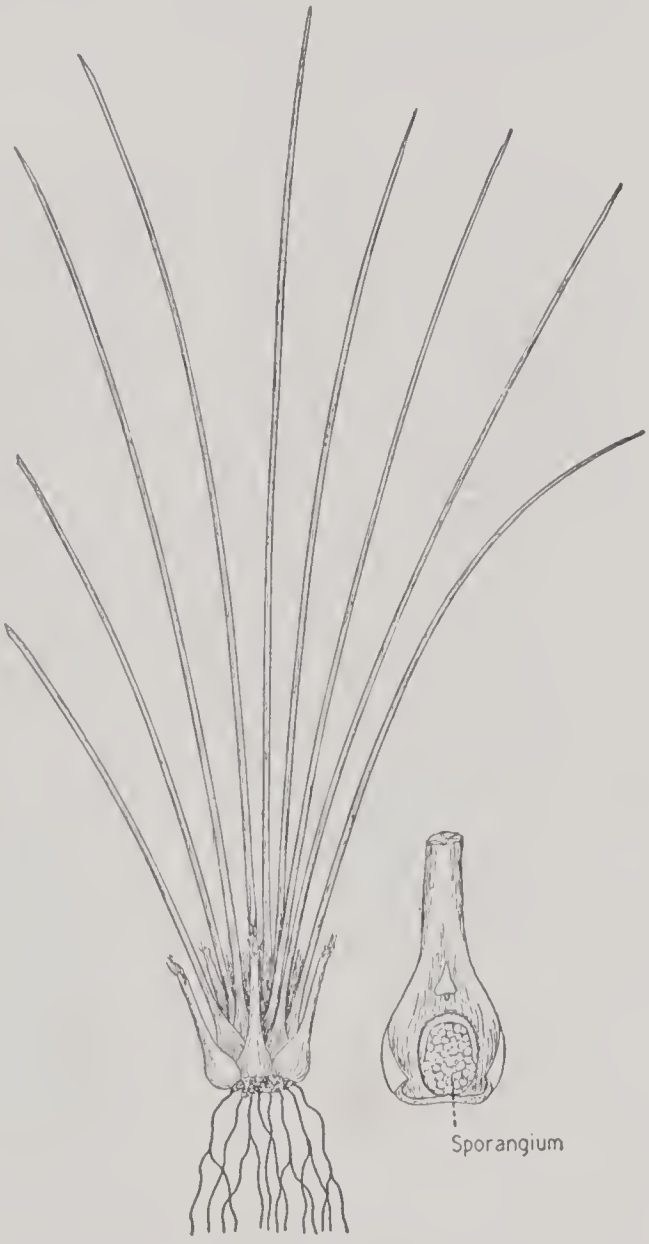


Fig. 31. Sketch, natural size, of a quillwort, *Isoetes*, another kind of pteridophyte. To the right is an enlarged view of the spore-bearing sporangium at the base of a leaf. (Weatherwax: Plant Biology.)

tects the embryo from heat, cold, drying, and from parasites; and they provide a means for the dispersal of the species over a wide area.

Gymnosperms. The gymnosperms have no flowers, but bear their seeds on the inner sides of scalelike leaves that are usually arranged spirally to form a cone. The gymnosperms are woody plants which do not differ greatly in their structural pattern from the woody angiosperms.

* Some angiosperms which seem to violate this rule and have exposed seeds—for example, wheat and sunflowers—really do have enclosed seeds, for the structure commonly called the seed is actually a fruit, enclosing the true seed.

At the present time the species of gymnosperms number only about 6000, but in former geologic times there were many more, and they were the dominant land plants. Today, the living gymnosperms are divided into four orders: the **conifers,** the **cycads,** the **ginkgos** and the **gnetales.** Three other orders are known only from fossil forms. Many of the plant fossils found in deposits of coal and once thought to be ferns, are now known to have produced pollen and seeds, and hence to have been spermatophytes. These are called "seed ferns."

Fig. 32. Photographs of cycads, members of one division of the gymnosperms. *Above, Cycas; below left,* a male plant of *Zania;* and *below right,* a mature, fruiting plant of *Zania.* This plant, found from Florida to Mexico, is the only cycad native to the United States. (Weatherwax: Plant Biology.)

Of the living gymnosperms, the **conifers,** which include the pine, cedar, spruce and fir trees, are the most successful biologically. The needle-like leaves of the evergreens are well adapted to withstand hot summers, cold winters and the mechanical abrasion of storms. Such trees develop two kinds of cones, one producing pollen and one producing eggs; The male cones release the pollen, which is carried by the wind to the female cones, where the eggs are fertilized. In some species, such as the pine, two summers and a winter pass before the fertilized egg develops into a mature seed ready to be shed.

The conifers are important economically as the source of more than 75 per cent of the wood used in construction, and in the manufacturing of paper and plastics. Some of them produce resins necessary for making turpentine, tar and oils. A few conifer seeds—for example, the pine "nuts"—are used as food, and the berries of juniper produce aromatic oils used for flavoring alcoholic beverages, such as gin.

The **cycads** live mainly in tropical and semitropical regions and have either short, tuberous, underground stems or erect, cylindrical stems above the ground. Their large, compound, divided leaves (Fig. 32) make them look very much like ferns or miniature palm trees, for which they are frequently mistaken.

The **ginkgo,** or maidenhair tree, is the only living representative of a once numerous and widespread order. It survived in China and Japan,

Fig. 33. Ginkgo twigs. *Left,* A cluster of mature seeds; *center,* a twig with leaves and young ovules; *right,* a twig with leaves and pollen cones. (Fuller, H. J.: The Plant World, Henry Holt and Co., Inc.)

where it was cultivated as an ornamental tree, because of its distinctive, fan-shaped leaves, which it sheds in the fall (Fig. 33). Recently, it was introduced into other countries. A given tree is either male or female and produces but one kind of cone. When an egg is fertilized and matures, the inner seed covering becomes hard, while the outer covering becomes soft and pulpy, with a rancid, foul odor. Therefore, when a tree produces many seeds at once, the odor is extremely offensive. For this reason, when ginkgos are planted in parks, care must be taken to ensure that all the trees in one region are of the same sex, so that seeds will not be produced.

The **gnetales** include some peculiar plants, among which are tropical trees or shrubs resembling angiosperms, except that they reproduce by means of cones. One of the strangest of these is the *Welwitschia,* found

in the desert in southwest Africa, and consisting of a short, thick trunk, partly imbedded in the soil, from which two long, flat, leathery leaves grow out along the ground (Fig. 34). Although the plant may live for centuries, it never produces more than these two leaves, which, subjected as they are to the sand and windstorms of the desert, eventually become very tattered.

Angiosperms. The **angiosperms,** or true flowering plants, are characterized by seeds which develop within a closed ovary. They are extremely diverse and widespread, ranging from the tiny duckweed with a body less than a tenth of an inch in length, and with no distinct root,

Fig. 34. Sketch of *Welwitschia* plants in their native habitat, the desert of southwestern Africa. These plants are gymnosperms, members of the group Gnetales. (After Kerner and Oliver. Weatherwax: Plant Biology.)

stem or leaf, but which produces tiny flowers and fruits, to trees exceeding 200 feet in height, and weighing hundreds of tons. Some angiosperms live completely under water, others in extremely arid deserts. The majority are autotrophic, but some, such as the orchid, Indian pipe and mistletoe, have little or no chlorophyll and so are partly or wholly parasitic. A few angiosperms have evolved devices for catching insects and other small animals, and hence are holozoic and carnivorous. Many angiosperms can complete an entire life cycle, from the germination of a seed to the production of new seeds, within a month, but others may require twenty or thirty years to reach sexual maturity. Some live for only one growing season; others live for centuries. The stems, leaves and roots present a bewildering variety of forms, but all angiosperms develop flowers which have a fundamental similarity of pattern. They differ from the gymnosperms in the abundance and prominence of the xylem vessels; in the formation of flowers and fruits; in the formation of a pistil through which the pollen tube grows to reach the ovule and egg (see p. 342) (in gymnosperms the pollen lands on the surface of the ovule and the pollen tube grows in directly); and in the further

reduction of the gametophyte generation to a few cells completely parasitic on the sporophyte.

The angiosperms are divided into two subclasses, the **monocotyledons** and the **dicotyledons,** which differ in the following ways:

(*a*) The embryo in the monocot seed has only one leaf, or cotyledon; the dicot embryo has two.

(*b*) The leaves of monocots have parallel veins and smooth edges; those of dicots have veins which branch and rebranch and, usually, edges which are lobed or indented.

(*c*) The flower parts of monocots—petals, sepals, stamens and carpels—exist in threes or multiples of three; dicot flower parts usually occur in fours or fives, or a multiple of one of those numbers.

(*d*) Bundles of xylem and phloem vessels are scattered throughout the stem of monocots; in dicots, the xylem and phloem vessels occur either as a single, solid mass, running up the center of the stem, or as a ring between cortex and pith.

There are a great many different families of both monocots and dicots, each of which usually takes its name from some conspicuous member. Among the 30,000 or so species of monocots are the grasses, palms, lilies, orchids and irises. The chief dicot families are the buttercup, mustard, rose, maple, cactus, carnation, primrose, phlox, mintbean, parsley and aster.

There is a difference of opinion about the evolutionary relationships of the spermatophytes, but many botanists regard the monocotyledons as having evolved from dicotyledon ancestors. Whether the angiosperms evolved from the gymnosperms or whether they both evolved independently from pteridophytes is debatable.

QUESTIONS

1. What is the outstanding way in which plants differ from animals?
2. Explain why green plants are dependent upon the sun for nourishment.
3. Exactly what part in photosynthesis does the energy from light play?
4. Why is respiration vital to life? Distinguish between the process of respiration and that of photosynthesis.
5. Without a transportation system, how do cells of the simple plants obtain nourishment?
6. What is tropism? Give an example from your own observation.
7. What is the relationship between a family and a species? Between a genus and a class? Between a phylum and a species?
8. What peculiar quality of the fungi sets them off from other plants?
9. What is meant by parasitism? Is it exemplified by lichens?
10. Distinguish between sexual and asexual reproduction.
11. What is a fruiting body? How does it differ from a true fruit?
12. Why was the process so long and difficult whereby land plants developed from marine plants?
13. Explain the function of leaves, stems and roots.
14. What is the important advance of the ferns over the mosses?
15. What is the distinguishing characteristic of the spermatophytes?
16. What is the fundamental difference between a pine tree and a maple tree?
17. To what phyla do the following belong, and in what important ways do they differ: (*a*) a tulip, (*b*) a mushroom, (*c*) moss, (*d*) bacteria, (*e*) grass, (*f*) an orchid, (*g*) a box hedge? Are any of these fundamentally similar? In what ways?

SUPPLEMENTARY READINGS

Fuller, H. J.: *The Plant World.* New York, Henry Holt & Company, Inc., 1941.
A well-illustrated description of the types of plants.

Holman, R. M., and Robbins, W. W.: *A Textbook of General Botany.* 4th ed. New York, John Wiley & Sons, Inc., 1939.
A more advanced presentation of plant structure and function.

Hylander, C. J.: *The World of Plant Life.* New York, The Macmillan Company, 1942.
An interesting survey of the variety of plant life.

Weatherwax, P.: *Plant Biology.* 2d ed. Philadelphia, W. B. Saunders Company, 1947.
A well-written and illustrated brief survey of botany.

CHAPTER 6

THE STRUCTURE AND FUNCTIONS OF A SEED PLANT

SINCE the spermatophytes are the most widespread, familiar and, for man, the most useful of plants, let us examine the structures of a typical seed plant—the root, stem, leaf and flower—and see how their functions are related.

I. THE ROOT AND ITS FUNCTIONS

The most obvious function of the root is to anchor the plant and hold it in an upright position; to do this, it branches and rebranches

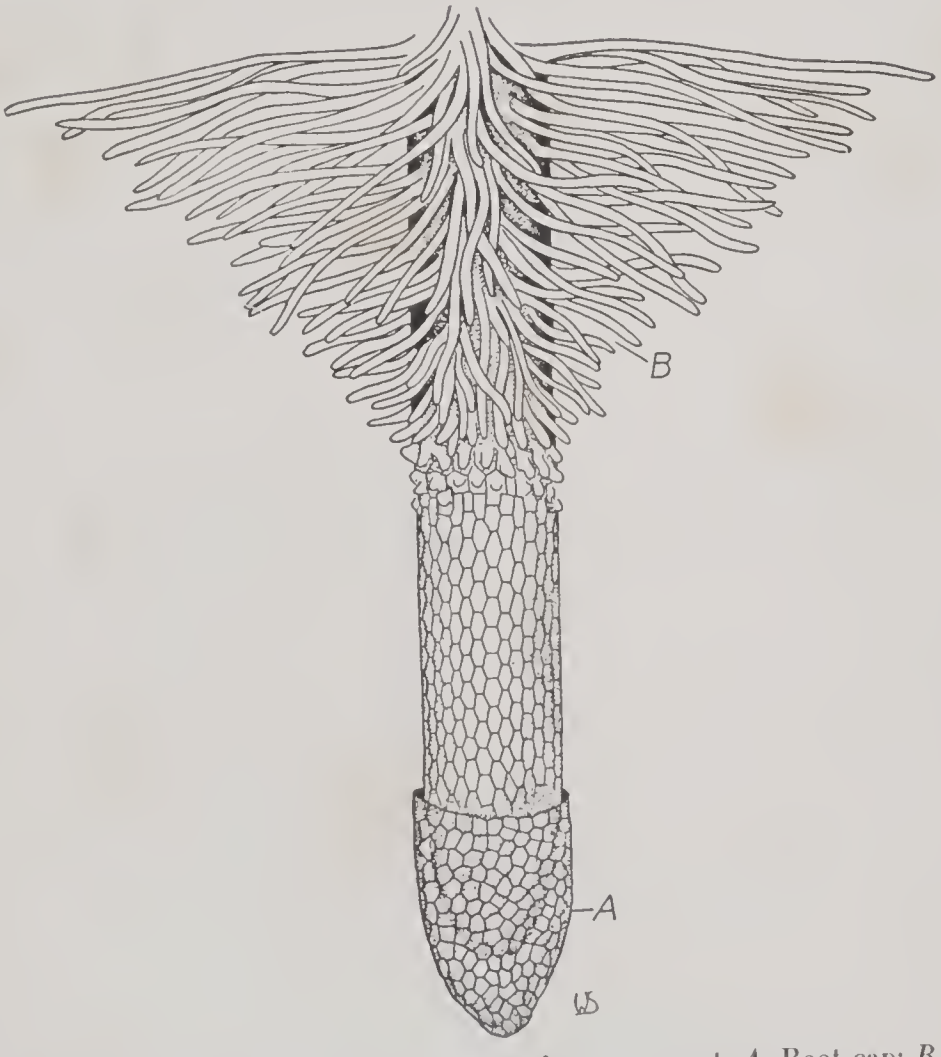


Fig. 35. Diagrammatic, enlarged view of the tip of a young root. *A*, Root cap; *B*, root hairs. (Fuller, H. J.: The Plant World, Henry Holt and Co., Inc.)

extensively through the soil. Although the depth of the roots seldom equals the height of the stem, the roots frequently extend farther to the side than the stem's branches, so that the total surface exposed by

them often exceeds that of the stem. The second, and biologically more important, function of the root is the absorption of water and minerals from the soil, and the conduction of these substances to the stem. In some plants—for example, carrots and beets—the roots have still another function as storage places for large quantities of food.

The tip of each root is covered by a protective **root cap**, a thimble-shaped covering of cells which fits over the rapidly growing embryonic (meristematic) region (Fig. 35). The outer part of the root cap is rough and uneven because its cells are constantly being worn away as

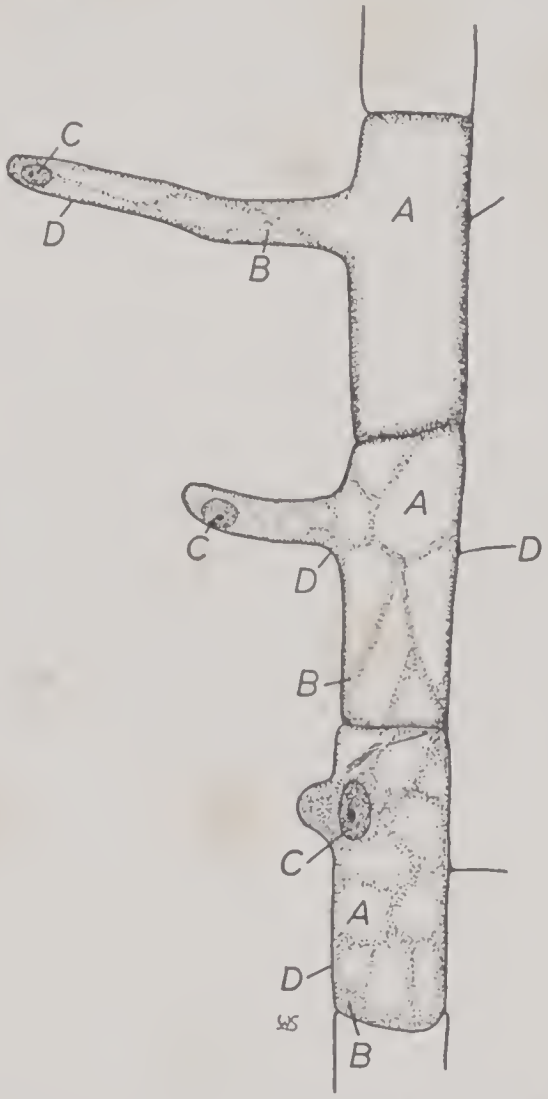


Fig. 36. Development of a root hair from an epidermal cell of a root: earlier stages below, later stages above. *A*, Vacuoles; *B*, cytoplasm; *C*, nucleus; *D*, cell walls. (Fuller, H. J.: The Plant World, Henry Holt and Co., Inc.)

the root pushes through the soil. Above the region of rapid cell division is another in which the newly formed cells elongate to the adult size. The embryonic and elongation regions together are seldom more than a millimeter or two in length, but nearly all the growth of the root occurs there.

Above this growing region is the **root hair zone** (Fig. 36), which is constantly being exposed to new regions of the soil. A root hair is a slender, elongated, lateral projection from a single epidermal cell, through which most of the water and minerals are absorbed. Any epidermal cell may absorb substances, but the surface exposed by a root hair is much larger and hence more effective than that of a single epi-

dermal cell. Root hairs are numerous; investigators have found as many as 2000 on a bit of corn root 1 mm. long. As the root elongates, the root hairs of the older region gradually die and make room for the new ones being formed, so that only a short segment of the root has living hairs at any one time.

A cross section of a root in the root hair region (Fig. 37) reveals a highly organized structure. The outermost layer of cells, the **epidermis,** produces the root hairs and protects the underlying cells. Just inside the epidermis is the **cortex** layer, made of large, thin-walled, roughly spherical parenchyma cells which serve as avenues for the conduction of minerals and water, and are important as storage places for food. A single layer of cells, the **endodermis,** separates the cortex from the underlying layers of vascular tissue. In the older parts of the root the endodermis is thick and contains a material which prevents the diffusion of water into the cortex. Just under the endodermis is a layer

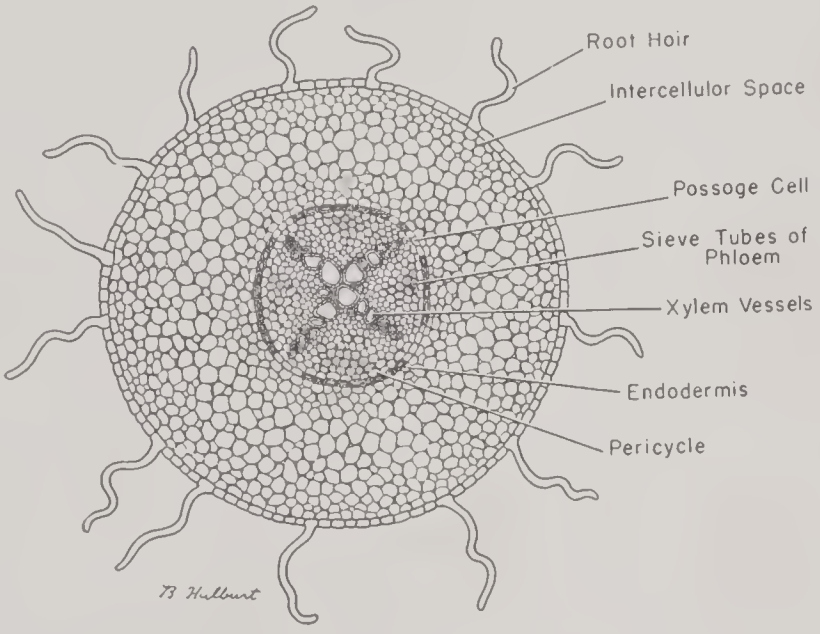


Fig. 37. Cross section of a root near its tip where root hairs are present

of cells, the **pericycle,** capable of growing and dividing to produce new cells which develop into branch roots. Within the pericycle lies the xylem, usually arranged in the form of a star, or like the spokes of a wheel, and composed of thick-walled, rounded conduction cells. Between adjacent points of the xylem star are small groups of phloem cells, smaller and thinner-walled than the xylem, which bring to the roots food manufactured in the leaves.

Since the water in the soil is a solution of inorganic salts, hypotonic to the protoplasm of the root hairs, it tends to enter the latter by osmosis. As the root hair cells take in water, they become, in turn, hypotonic to the underlying cells of the cortex, and water passes inward, via the various tissues of the root, to the ducts of the xylem. The liquid in the xylem, the plant **sap,** containing sugars and salts, is hypertonic to the surrounding tissues and tends to absorb water from them. The water entering the xylem increases the pressure of the liquid within the ducts, just as water entering a sugar-filled cellophane membrane does (p. 19). This **root pressure** forces the sap to flow upward through the root and stem. Since water is constantly escaping from the leaves, and

new sugars are formed in the leaves and sent via the phloem to the roots, the hypertonicity of the root sap is maintained and further absorption of water is possible.

The entrance of inorganic salts is accomplished partly by simple diffusion, since the concentration of salts in the soil is usually higher than that in the root cells. But certain roots, at least, are able to take in

Fig. 38. Types of root systems in plants. *A*, The diffuse root system of a grass; *B*, the tap root system of a carrot. (Fuller, H. J.: The Plant World, Henry Holt and Co., Inc.)

inorganic salts by processes—as yet not well understood—which require the expenditure of energy. Because the sap contains these inorganic salts in rather small amounts, large volumes of it must flow to the stems and leaves to provide the necessary nutrients.

Botanists distinguish two common types of roots: **diffuse roots,** made of many slender branches of nearly equal size, and **tap roots,** large, single roots, usually growing directly downwards, with many, much smaller, secondary rootlets (Fig. 38).

II. THE STEM AND ITS FUNCTIONS

The stem, which in a tree includes the trunk, branches and twigs, is the connecting link between the roots, where water and minerals enter

the plant, and the leaves, which manufacture food. The vascular tissues of the stem are thus continuous with those of root and leaf, providing a pathway for the exchange of materials and enabling the stem to support the leaves in a position to receive maximum sunlight. Roots and stems are sometimes confused, for many kinds of stems grow underground and some roots grow in the air. Structurally the two are quite different: stems, but not roots, have nodes giving rise to leaves, and the tip of a root is always covered by a root cap, whereas the tip of a stem is naked, unless it terminates in a bud. Moreover, there are certain differences in the arrangement of xylem and phloem in the two structures.

Plant stems are either **herbaceous** or **woody.** The soft, green, rather thin herbaceous stems are typical of plants called **annuals.** Such plants start from seed, develop, flower, and produce seeds within a single growing season, dying before the following winter. Another type of herbaceous plant is the **biennial,** which has a two-season growing cycle. During the first season, while the plant is growing, food is stored in the root. Then the top of the plant dies and is replaced by another top, which produces seeds during the second growing season. Carrots and beets are biennials.

Quite different from both the herbaceous annuals and biennials are the woody **perennials,** which live longer than two years and have a thick, tough stem, or trunk, covered with a layer of cork. A **tree** is a woody-stemmed perennial that grows some distance above ground before it branches, and so has a main stem or **trunk.** A **shrub** is a woody perennial with several stems of roughly equal size above the ground line. It is generally believed that woody stems are more primitive than herbaceous ones, all the available evidence indicating that the first true seed plants were woody-stemmed perennials. In past geological ages such plants grew as far north as Greenland, but with the change in climate toward the end of the Mesozoic era, some of these plants were killed by the advancing cold and the species forced to retreat toward the equator. Still other woody plants became herbaceous by evolving a life cycle in which growth and flowering were completed in the warm summer of a single year, the rigors of the winter being withstood by cold-resistant seeds.

The herbaceous stem tissues are arranged around the bundles of xylem and phloem, but are different in monocots and dicots. In the stem of a dicot, such as the sunflower or clover, there is a circular arrangement of the xylem and phloem bundles which subdivides the stem into three concentric regions: the outer cortex, the **vascular bundles,** and the central core (the **pith**) of colorless parenchyma cells which serve as storage places. Each vascular bundle has an outer cluster of phloem cells and an inner cluster of xylem cells, separated by a layer of growing, meristematic tissue, the **cambium** (Fig. 39). Between the vascular bundles lie groups of cells known as **medullary rays,** which extend radially from the vascular region to both pith and cortex, and distribute materials from the xylem and phloem to those inner and outer parts.

The stems of woody plants resemble herbaceous ones during their first year of growth, but in each successive year the cambium forms

an additional layer of xylem and phloem. The yearly deposits of xylem form the annual rings (Fig. 40). These can be distinguished because the xylem vessels formed in the spring of the year are larger, and hence appear lighter, than those formed in the summer. Only the youngest, outermost layer of xylem, known as the **sapwood**, carries sap to the

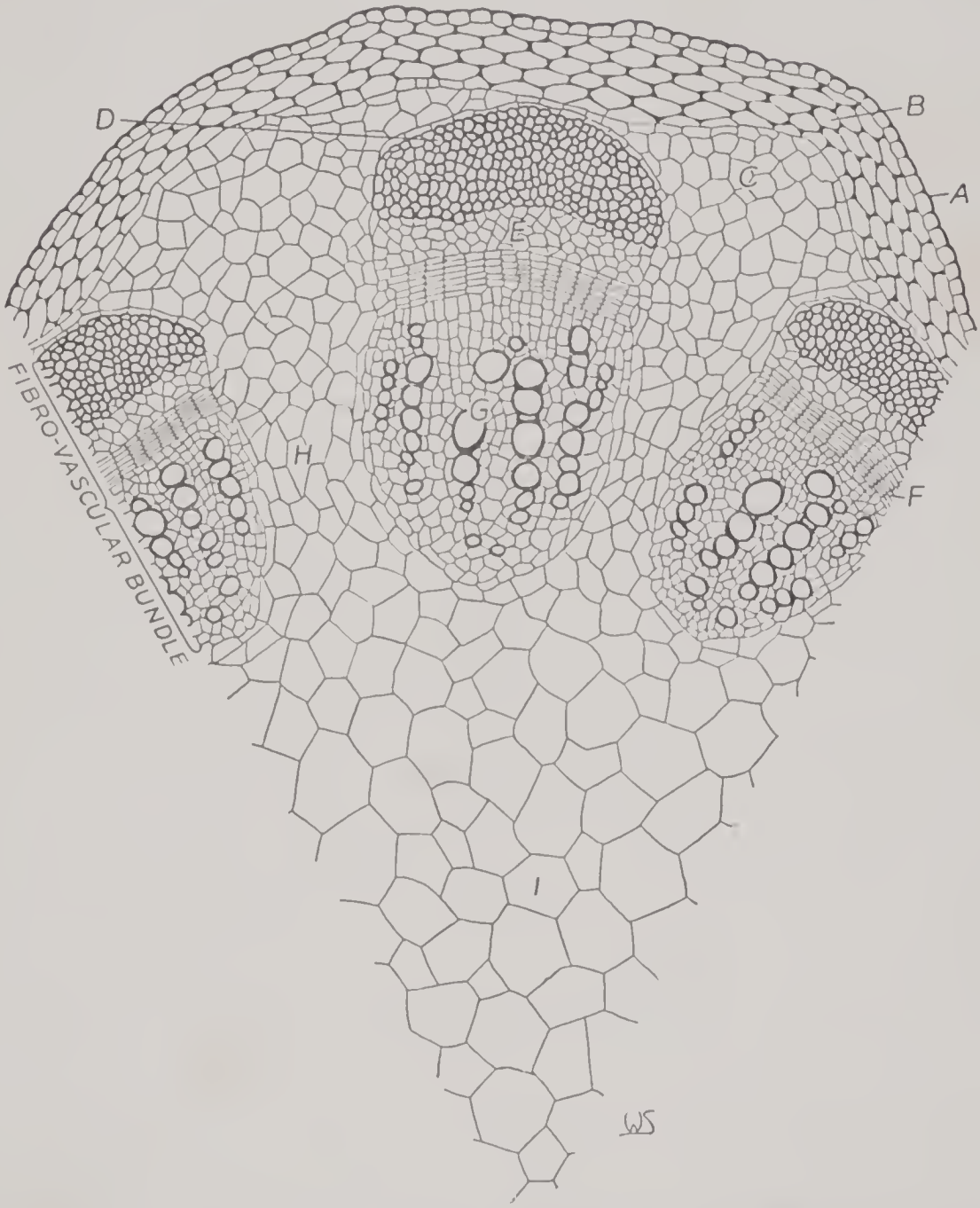


Fig. 39. Part of a cross section of a stem from a herbaceous dicotyledon, clover. *A*, Epidermis; *B*, collenchyma cells of the cortex; *C*, parenchyma cells of the cortex; *D*, pericycle fibers; *E*, phloem; *F*, cambium; *G*, xylem; *H*, ray; *I*, pith. (Fuller, H. J.: The Plant World, Henry Holt and Co., Inc.)

leaves; the inner layers of dead, hard xylem cells and fibers, known as the **heartwood**, increase the strength of the stem, in order to accommodate the increasing load of foliage as the plant grows. The width of the annual rings varies according to the climatic conditions prevailing when the ring was formed, so that it is possible to infer what the climate was at a particular time, several hundred or even thousands of years ago, by examining the rings of old trees. An interesting application of this

sort of study is the investigation to determine approximately when the Indian pueblos of the Southwest were built, by comparing the annual rings of the logs used in their construction with those of trees whose year of felling is known.

The cambium is also important in the healing of wounds. When the stem's outer layer is removed through injury, the cambium grows over the exposed area, and differentiates into new xylem, phloem and cambium, each of which is continuous with the same type of tissue in the uninjured part of the plant. The cells of the outer cortex of most woody plants undergo division to form a second, **cork cambium;** since the divisions usually occur unequally and irregularly, the bark produced is rough and full of ridges. These outer cork cells become impregnated with a waterproof, waxy material and eventually die and fall off, partly

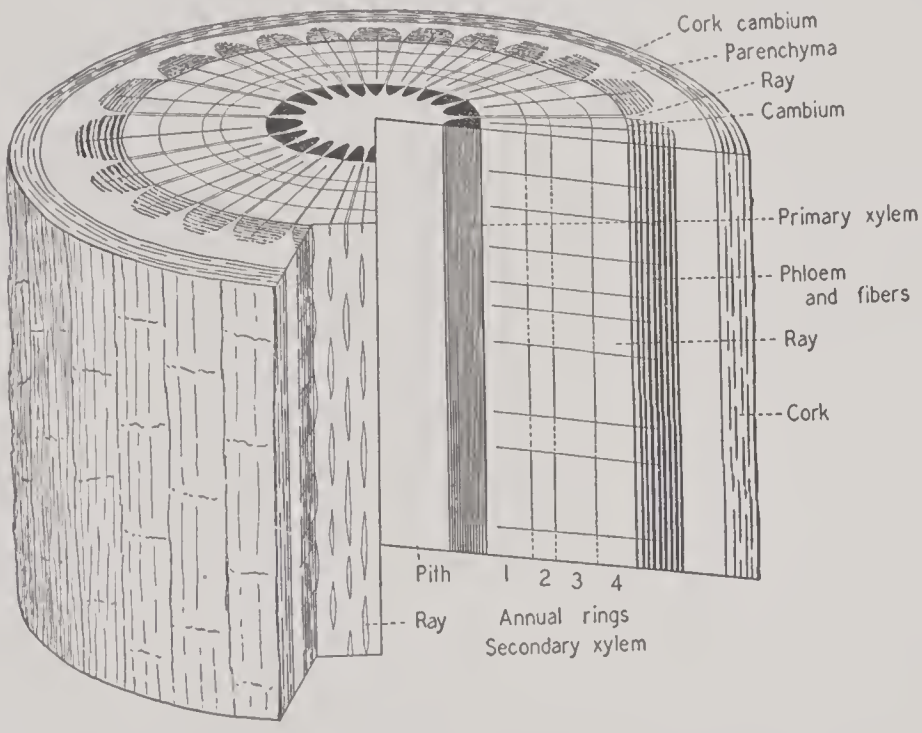


Fig. 40. Diagram of a four year old woody stem, showing transverse, radial and tangential sections. (Weatherwax: Plant Biology.)

under the stress of wind and rain, partly because of the outward pressure of the growing tissues within.

The epidermis of a young twig has openings (stomata) like those of leaves, through which gases may enter and leave. As the epidermis is replaced by the cork layer, special openings, called **lenticels,** develop in place of the stomata to permit the movement of gases into and out of the stem. But unlike the stomata, which can open and close as needed, the lenticels remain permanently open.

The stems of monocots are characterized by bundles of xylem and phloem cells which, instead of being arranged in a continuous, circular layer, are scattered throughout the stem. As in the dicots, the phloem is always in the outer part of the bundle, and the xylem is in the inner part. Most monocots have no layer of cambium, and the cells of all the tissues are produced from the bud.

On the surface of an active, growing stem are a number of familiar

structures, the most obvious of which are the buds and leaves (Fig. 41). The point on the stem where a leaf develops is called a **node,** and the section between two nodes is called an **internode.** Internodes may be short or up to several inches in length. In the upper angle of the point of junction of a leaf with the stem, a bud usually appears, called a **lateral** or **axillary** bud to distinguish it from the **terminal** bud at the tip of the stem. A bud consists of a number of embryonic leaves, a growing point, and a series of outer protective scales, which in some species give off a thick, gummy secretion, and have a dense covering of hairs

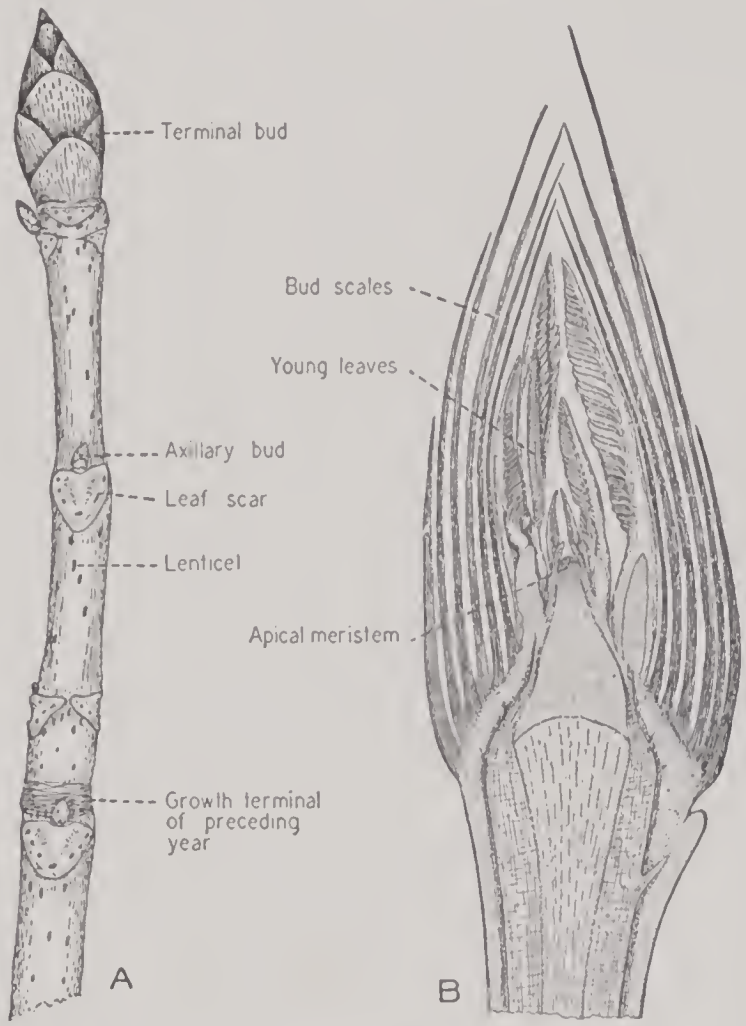


Fig. 41. *A*, Buckeye twig, showing buds and scars; *B*, longitudinal section through a terminal bud from a hickory tree. (Weatherwax: Plant Biology.)

to increase their protective value. In some species the leaves within the buds are fairly well developed, so that their ultimate shape can be distinguished; in others they are shapeless rudiments.

When a terminal bud begins to grow in the spring, its covering scales fall off, leaving a ring of scars. These scars, which mark the position of the end of the stem at the completion of the season, may remain visible for several years, so that it is possible to determine the age of a twig by counting its terminal bud scars.

The over-all shape of a tree or shrub is determined by the position, arrangement and relative strength or activity of the terminal and axillary buds. Thus, in a tree with a strong terminal bud, such as a poplar tree, the twig produced by the terminal bud is much more vigorous

than those produced by lateral buds, and the main trunk and its branches grow straight upwards. But plants with vigorous lateral buds give rise to strong, horizontal branches, resulting in a spreading shape.

In addition to these, and the bud scars and lenticels already mentioned, other structures visible on the surface of a twig are the **leaf scars,** left when the stalk of a leaf breaks away from the twig, and **fruit scars,** left in a similar way by the breaking off of fruit.

It is possible to show experimentally that in the stem, water and salts are carried upward in the xylem, and organic materials are carried downward in the phloem. If a cut is made all around a stem, deep enough to penetrate the phloem and cambium, but not the xylem, the leaves remain in good condition and do not wilt for some time, indicating that they are receiving water by way of the xylem. The parts of the plant above the injury also continue to grow in diameter, showing that they are receiving food products from above, via the phloem but the parts below the injury cease growing and sooner or later die By special techniques it is possible also to cut the inner xylem of a stem without disturbing the phloem. When this is done, the leaves wilt and die immediately, indicating again that almost all the water reaches them via the xylem. Furthermore, if the cut end of a stem is placed in water containing a dye, the xylem vessels become colored.

Two factors are mainly responsible for the transport of water by the xylem: root pressure and transpiration. Transportation of food by the phloem is due in part to simple diffusion, and in part to energy-consuming processes similar to those involved in the intake of minerals by the roots.

III. THE LEAF AND ITS FUNCTIONS

Since the purpose of leaves is to facilitate photosynthesis, they are usually broad, flat structures which expose a large surface to sunlight. The leaf of dicots consist of a stalk, called the **petiole,** by which it is attached to the stem, and a broad **blade,** which may be one simple structure, or a compound one, with two or more parts. The petiole may be short, and in some species is completely lacking. Like a stem in cross section, it is composed of vascular bundles, attached at one end to those of the stem, at the other end to the blade. Thus it forms the midrib of the leaf and branches into a network of veins.

A microscopic section through a leaf (Fig. 42) shows it to be composed of several types of cells. The outer cells, both top and bottom, make up a colorless, protective layer called the **epidermis** which secretes the waxy material, cutin. The epidermal cells—thin, tough, firm-walled and translucent—are well constructed to give protection and yet admit light. Scattered over the epidermal surface are many small pores (stomata), each surrounded by two guard cells which, by changing their shape, control the escape of water and the exchange of gases. In contrast to the epidermal cells, the guard cells contain chloroplasts. There are fifty to 500 stomata per square millimeter of leaf, many more on the lower than on the upper surface. The pairs of guard cells are so constructed and arranged that when there is plenty of water in the leaf, they are turgid and remain apart, so that the stomata are left open. When the loss of water is excessive, they become deflated, wilt, and

come together to close the stomata openings, thereby conserving the remaining water.

Most of the space between the upper and lower layers of the leaf epidermis is filled with thin-walled cells, called **mesophyll**, which are full of chloroplasts. The mesophyll cells fit together rather loosely with much air space lying between them. In most leaves the mesophyll layer next to the upper epidermis is made of cylindrical cells, called **palisade cells**, so arranged that their long axes are perpendicular to the epidermal surface.

The veins of a leaf branch and rebranch frequently to join one another in an extremely fine network, so that no mesophyll cell is far

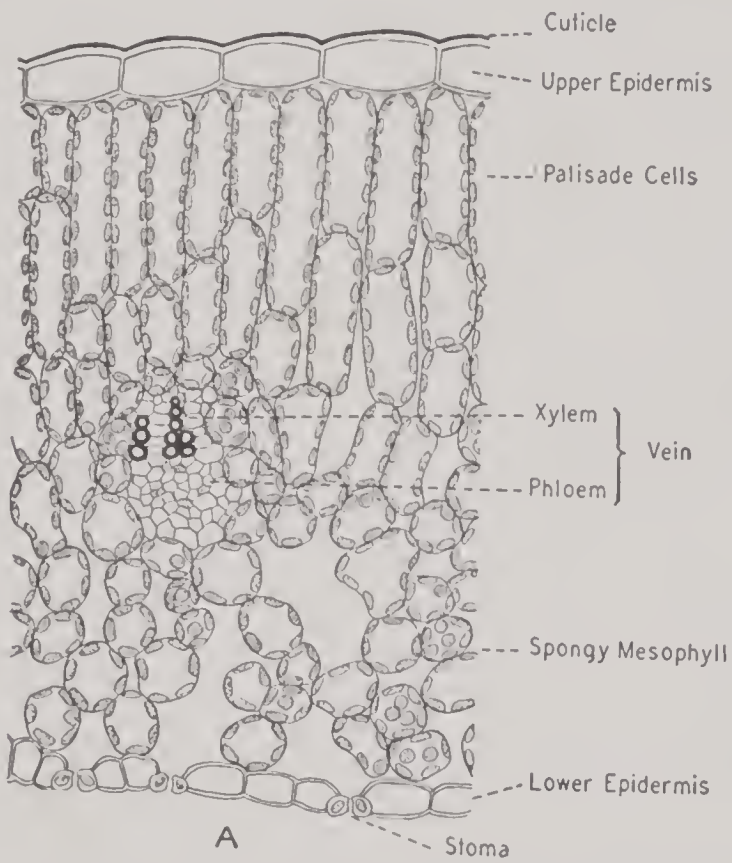


Fig. 42. Section through a lilac leaf, showing a small vein. (Weatherwax: Plant Biology.)

from a vein. The xylem of each vein lies above the phloem, and in the smaller veins there may be only a few xylem ducts and a few phloem sieve tubes.

The fall of leaves in the autumn of the year is brought about by changes at the point where the petiole is attached to the stem. A special layer of cells extends across the base of the petiole, made up of cells so loosely joined together that they constitute a weak spot. The part next to the stem becomes corklike and forms a protective layer which remains when the leaf falls off. When this layer has formed, the petiole is held on only by the epidermis and the easily broken vascular bundles. The change in color of the leaves is effected partly by the decomposition of the green chlorophyll, which exposes the yellow xanthophyll and orange carotene, previously hidden by the green pigment, and partly by the formation of red and purple pigments—anthocyanins—in the cell sap.

1. **Transpiration.** Since the leaves of a plant are normally exposed to the air, they must lose moisture by evaporation if the air is dry: the sun's heat vaporizes the water from the surfaces of the mesophyll cells, and the resulting water vapor passes through the stomata and escapes. This loss of water is called **transpiration.** The process may occur in all parts of a plant exposed to air, but most of it takes place in the leaves, which can regulate its rate to some extent by opening or closing the guard cells. In sunlight an average plant will transpire about 50 cc. of water per square meter of leaf surface per hour. This means that a single corn plant uses more than 50 gallons of water in a growing season, and a medium-sized tree transpires that much in a single day. An acre of many different crops takes 500 to 1500 tons of water from the soil, and the water vaporized from the leaves of trees in a forest is enough to influence significantly the rainfall, humidity and temperature of the region. The plant cannot close its stomata completely on a hot, dry day and so prevent transpiration, for that would prevent the intake of carbon dioxide necessary for photosynthesis.

Transpiration contributes to the economy of the plant not only by cooling the leaves, in a manner analogous to the evaporation of sweat in animals, but by concentrating in the leaves the dilute solutions of minerals absorbed by the roots, and by assisting the upward movement of water through the stem.

When it was discovered that all the water used by a plant enters through the roots, and that none comes in through the leaves, botanists wondered how the terrific pressures necessary to force water to the tops of tall trees could be generated. At present it is believed that the ascent of sap is brought about by both transpiration and root pressure. Root pressure is the positive force generated by the hypertonicity of the sap in the roots to the water in the surrounding soil. It was formerly believed that the pressure so generated by the roots was comparatively small, but recently it was found that an error lay in the method of measurement. With better techniques it was proved that even small plants, such as the tomato, can generate a root pressure of 12 atmospheres, enough to move water to a height of 384 feet. In the spring, before leaves have been formed, root pressure is almost the sole cause of the rise of sap. In the summer it rises much more rapidly, aided by the process of transpiration. Since water is constantly evaporating from the surface of the leaf, and the leaf cells are continually producing sugar, they are hypertonic to the sap in the veins of the leaf and consequently draw water from the upper ends of the xylem vessels. The negative pressure generated in this way may be as much as 20 atmospheres. The water columns, being under tension from above, are slightly stretched, but water molecules have a tendency to cling together, imparting a considerable tensile strength to the slender water column within a xylem vessel. Thus transpiration provides the pull at the top of the column, and the tendency for the water molecules to stick together, carrying this force through the length of the stem and roots, results in the elevation of the whole column of sap. Only about 1 per cent of the water reaching the leaf is used for photosynthesis; the rest evaporates from the surface in transpiration.

IV. THE STORAGE OF FOOD

Although in sunlight a green plant may produce more than twenty times as much food as it is using at the moment, at other times—during the night and winter—it consumes much more than it makes and therefore must accumulate reserves to tide it over periods when photosynthesis cannot be carried on. Plants deposit stores of food in their seeds to carry the embryo through until the seed has sprouted and the new plant has developed a functional root, stem and leaf. Plants which shed their leaves each fall must put away a reserve of food in the stem or root to carry it through the winter and provide energy for the growth of new leaves in the spring. This stored food must be in some insoluble form lest it diffuse away, and the usual form of storage is starch, deposited in the parenchyma of the root and stem. It is primarily this starch which provides the food value of potatos, onions, carrots, turnips, sweet potatos, and so on.

V. THE ECONOMIC IMPORTANCE OF PLANTS

We are completely dependent upon plants, both directly for food and indirectly for the food they supply to the animals from which we get our protein. Food, seasonings, beverages, as well as a variety of drugs, are derived from all parts of plants: roots (radishes, sarsaparilla, sweet potatoes); stems (garlic, sugar cane); leaves (lettuce, spinach); flowers (artichokes); seeds (corn, nuts, cocoa, coffee, nutmeg, mustard); and fruits (berries, squash, eggplant, apples).

The list of nonfood products used in everyday life—including such things as paint, rubber, soap and cotton, and representing a diversity of plant organs and secretions—is almost endless.

QUESTIONS

1. What two important functions do roots perform? What is a third function performed by some roots?
2. What is sap?
3. What are the important structural and functional differences between a root and a stem?
4. What is an "annual?"
5. Are "biennials" herbaceous or woody?
6. Why can the age of trees be determined from their rings?
7. Why does a plant wilt if it does not receive sufficient water?
8. What is transpiration, and why is it important?
9. How does water reach the top of tall trees?

SUPPLEMENTARY READINGS

Meyer, B. S., and Anderson, D. B.: *Plant Physiology*. New York, D. Van Nostrand Company, Inc., 1939.
One of the standard texts of plant physiology.

Miller, E. C.: *Plant Physiology*. 2d ed. New York, McGraw-Hill Book Company, Inc., 1938.
A detailed, advanced reference text.

Weatherwax, P.: *Plant Biology*. 2d ed. Philadelphia, W. B. Saunders Company, 1947.
A clear and interesting discussion of the anatomy and functioning of seed plants.

CHAPTER 7

THE ANIMAL KINGDOM

TO CATALOGUE the vast array of animals, zoologists use a classification system similar to the one used by botanists, consisting of species, genera, families, orders, classes and phyla. We noted in Chapter 5 that a good classification must be natural, based upon the observation of similarities of structure and development. It is not proper to classify bats with birds because they both happen to fly, or whales with fishes because they both live in the sea. Studies of the anatomy and development of bats and whales show them to have many characteristics in common, and indicate their origin in similar, primitive ratlike or shrewlike mammals. Thus both are members of the class Mammalia. Birds and fishes, which differ as much from bats and whales as from each other, belong to different classes—Aves and Osteichthyes, respectively.

In the study of taxonomy, then, superficial, accidental similarities must be differentiated from the significant, fundamental ones. Those structures of various animals which arise from common rudiments and are similar in basic plan and development are called **homologous. Analogous** structures, in contrast, are similar only in function. Accordingly, the arm of a man, the wing of a bird and the pectoral (front) fin of a fish (Fig. 43) are all homologous, with a basically similar structural plan and similar embryonic origins. But the wing of a bird and the wing of a butterfly are simply analogous, enabling their possessors to fly, but having no developmental processes in common. Structures may be both homologous and analogous; for example, the wings of birds and bats have a similar structural plan and development, as well as the same function. The study of structures and their development to prove homologies often plays an important part in determining the relationship between animals.

Because all animals have essentially the same problems to solve in order to survive, there is a basic unity of life, so that a discovery about one form has universal application. It is obvious that rats, rabbits and guinea pigs are similar enough to man so that experiments on their digestive, circulatory and excretory systems contribute to our understanding of the corresponding systems in man. But it is not so obvious that much of our knowledge of nerve action can and does come from experiments on squid nerves, that experiments on the heart of the horseshoe crab can give us information about the human heart, and that observations of the toadfish kidney are useful in understanding the human excretory system.

In Chapter 4 we found that the bodies of higher animals, such as man, have elaborate systems composed of organs, and that these, in turn, are made of tissues, which are aggregates of cells made of protoplasm. In

the evolution of the higher from the lower forms this organization was built up gradually, and today some of the lower forms illustrate the

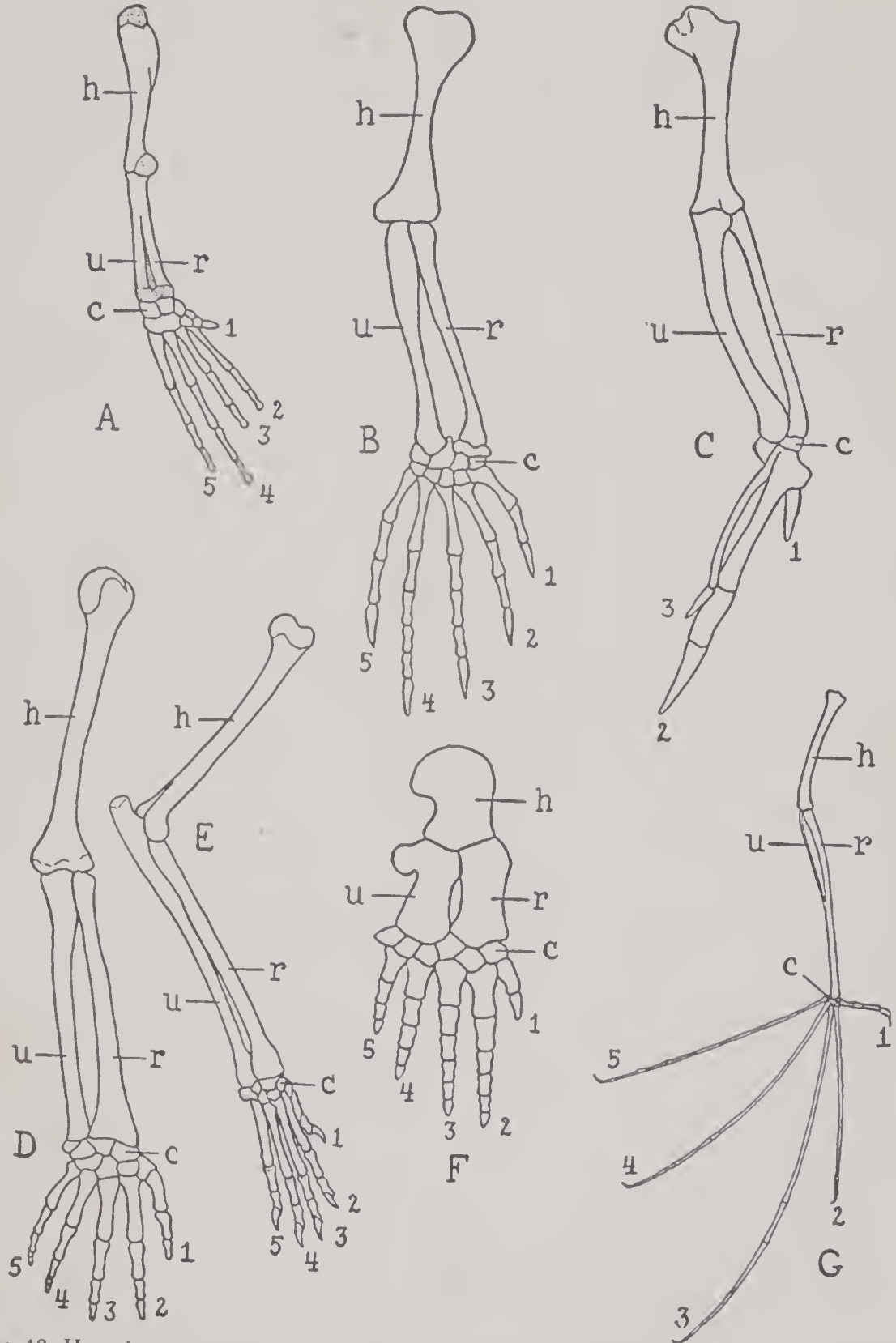


Fig. 43. Homologous bones of the forelimbs of various vertebrates: *A*, frog; *B*, lizard; *C*, bird; *D*, man; *E*, cat; *F*, whale; *G*, bat; *h*, humerus; *r*, radius; *u*, ulna; *c*, carpals; *1–5*, digits. (Marsland and Plunkett: Principles of Modern Biology, Henry Holt and Co., Inc.)

steps in the process: protozoa represent the **protoplasmic** level of organization, sponges the **cellular** level, coelenterates the **tissue** level, and flatworms the **organ** level. In the proboscis worm we have the most

primitive example of the **organ system** level of organization, which reaches a high development in man.

I. THE BASIS FOR ANIMAL CLASSIFICATION

The differences which distinguish related species, such as panthers and leopards, are usually minor and superficial—such as body color, proportion, and so on—but the main divisions of the animal kingdom, the phyla, are differentiated by basic characteristics which usually are not unique for a single phylum, but occur in *unique combinations* in various ones. Some of the factors basic to the determination of an animal's classification are as follows:

(*a*) The presence or absence of cellular differentiation. Animals may be either single-celled (the protozoa) or composed of many kinds of cells, specialized to perform particular tasks in the body's economy. In all the higher animals, collectively known as the **Metazoa,** cells are differentiated and specialized.

(*b*) The type of symmetry present, whether spherical, radial or bilateral (see p. 47).

(*c*) The number of germ layers. Some of the metazoa have only two embryonic cell layers or "germ layers"—an outer ectoderm, and an inner entoderm, which lines the digestive tract; others have these plus a third, the mesoderm, which lies between the ectoderm and entoderm, and comprises the rest of the body.

(*d*) The type of body cavity. In the lower many-celled animals the body is essentially a double-walled sack surrounding a single cavity with only one opening to the outside, the mouth. The higher animals have two cavities, their bodies being constructed on a tube-within-a-tube plan. The inner tube, or alimentary canal, is lined with entoderm, and opens at both ends, the mouth and anus; the outer tube, or body wall, is covered with ectoderm. Between the two tubes the second cavity, or **celom,** lies within the mesoderm and is lined by it.

(*e*) The presence or absence of segmentation. The members of several phyla are characterized by the fact that their bodies consist of a row of segments, each of which has the same fundamental plan, with or without variation, as the segments in front and behind. In some segmented animals, such as man and most vertebrates, the segmental character of the body is obscured. In man the bones of the spinal column—the vertebrae—are among the few remaining, clearly segmented parts of the body.

(*f*) Unique features. Although there are few structures which belong exclusively to one phylum of the animal world, a few animals do have unique qualities which aid in their classification. For example, the coelenterates alone have stinging cells (nematocysts); the echinoderms have a peculiar "water vascular system" found nowhere else; and, although many kinds of animals have a nervous system, only the chordates (with which man belongs) have a dorsally located, hollow nerve cord.

Animals are not classified according to the environment in which they live, but some of them are found in only one type of habitat; the

members of certain phyla always live in the sea, while the members of others are always parasitic, and so on.

II. THE PROTOPLASMIC LEVEL OF ORGANIZATION

1. **The Phylum Protozoa.** Our first phylum is made up exclusively of single-celled animals which, though structurally simple, are functionally complex. There is some division of labor within the single cell, but, on the whole, the protoplasm functions as a unit to perform all the life activities carried on by the many-celled body of higher animals—digestion, respiration, circulation, excretion, locomotion and reproduction. Hence the protozoa are said to be organized on the protoplasmic level.

All 15,000 or so species of protozoa are tiny, most of them microscopic, although a few are big enough to be seen with the naked eye (some of the largest amebas are 1 mm. long). In spite of the fact that many multiple-celled animals are smaller than the larger protozoa, the latter more closely resemble the primitive ancestor of all animals than do any of the many-celled animals, for that organism undoubtedly was single-celled. The present-day flagellates constitute a bridge between the plant and animal kingdoms, and are believed to be the protozoa closest to the ancestral stem of both. Some of them have chlorophyll and are holophytic; others, lacking chlorophyll, capture their own food and hence are holozoic; while still others are both. Some forms that normally have chlorophyll lose it if kept in the dark, and become holozoic. It is obvious, then, that at this primitive level the distinction between plant and animal disappears.

Because the body of the protozoan *Amœba proteus* (Fig. 85) consists of nothing but a clear mass of shapeless, naked, gelatinous protoplasm, containing a nucleus and protoplasmic granules, it is often used to study the characteristics of protoplasm. The nucleus of this tiny animal occupies no fixed position in the cell. It is pushed around within the protoplasm as the animal moves, which it does by pushing out temporary protoplasmic projections, called **pseudopods** (false feet), from the surface of the cell. When this occurs, additional protoplasm flowing into the pseudopods enlarges them until finally all the protoplasm has entered and the animal as a whole has moved. The mechanism responsible for the flow of protoplasm in ameboid motion is unknown. By close observation of a moving ameba one can see that not quite all the protoplasm moves; actually, a stable gel layer at the surface surrounds the central core of liquid, flowing protoplasm. Experimental evidence indicates that protoplasm in the gel state can contract, thus squeezing the contained sol and pushing it forward, a process which is possible because the tip of the pseudopod lacks a gel layer. As the liquid protoplasm reaches the tip, it is pushed to the sides by the protoplasm behind, and converted from a sol to a gel, to form that part of the wall. Meanwhile, at the posterior end of the ameba, the gel walls are converted to a sol to be pushed along. The process of ameboid motion, as well as the chemical reactions supplying the energy for it, is probably fundamentally similar to muscular contraction, which also depends upon reversible changes from sol to gel. The white blood cells of man and other higher animals move by ameboid motion.

The pseudopods are used also to capture food (Fig. 103), two or more of them moving out to surround and engulf a bit of debris, another protozoan, or a small, many-celled animal. The engulfed food is surrounded by a food vacuole, and the encircling protoplasm secretes digestive enzymes to break down the food for absorption.

Respiration is an uncomplicated process in amebas and other protozoa, since they live in a liquid environment and can take in oxygen and give off carbon dioxide by diffusion. Excretion also occurs by this simple method. Many protozoa, amebas as well as others, have a **contractile vacuole,** a cavity in the protoplasm that regularly fills with water from the surrounding medium, and empties it out again. This structure is believed to be not an excretory organ, but simply a pump for the removal of the excess water constantly entering by diffusion. The protoplasm of a fresh-water ameba has a higher concentration of dissolved materials—salts, sugar, and so on—than the surrounding water, so that water tends to pass into it by osmosis. Without a pump to

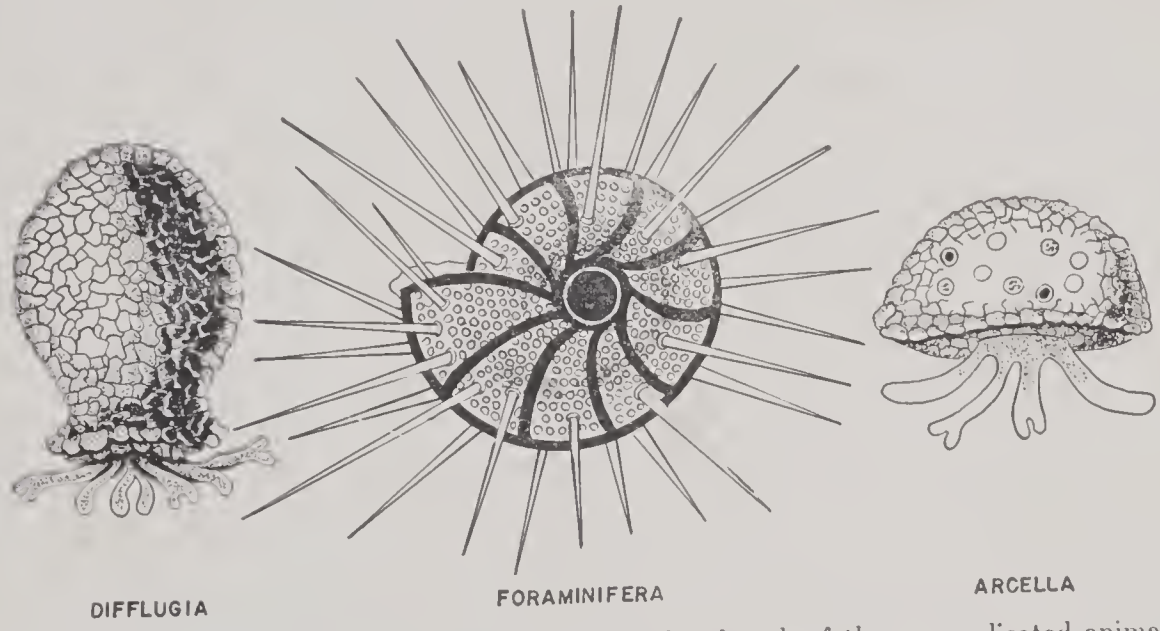


Fig. 44. Some types of amebas with shells. The body of each of these complicated animals consists of a single cell. (Hunter and Hunter: College Zoology.)

remove excess water, the ameba would soon swell and burst, as our blood cells do when they are placed in fresh water. In contrast, most marine protozoa do not have or need a contractile vacuole, since the concentration of salts in the sea water is about the same as that in their protoplasm.

The *Amœba* belongs to the class **Sarcodina** (fleshlike) containing many other protozoa, all of which move about by means of pseudopods. Some of them, such as the species causing amebic dysentery in man (p. 407), are parasitic. Other, free-living species secrete hard shells around their body, or cement sand grains together into a protective layer around their naked protoplasm. The ocean contains untold trillions of ameboid protozoa called **foraminifera** (Fig. 44), which secrete chalky, many-chambered shells with pores through which the animal extends its pseudopods. The dead foraminifera sink to the bottom of the ocean and form a gray mud which is gradually transformed into chalk. The famous white cliffs of Dover were formed in this way by

fossil foraminifera. Because deposits of these fossils are frequently associated with petroleum deposits, they are of great importance to geologists examining rock strata for signs of oil. Still other ameboid protozoa, called **radiolaria**, secrete elaborate and beautiful skeletons made of silica. The skeletons eventually become mud on the ocean floor, and are sometimes converted into siliceous rock such as flint.

A second class of protozoa, the **Ciliata**, is typified by the *Paramecium* (Fig. 85). This animal, unlike the ameba, has a definite and permanent shape—clearly rounded in front and pointed in the rear—due to a sturdy, though flexible, outer covering secreted by the cell. The surface of the cell is covered by some 2500 fine, protoplasmic hairs, called **cilia**, which extend through pores in the outer covering and move the animal

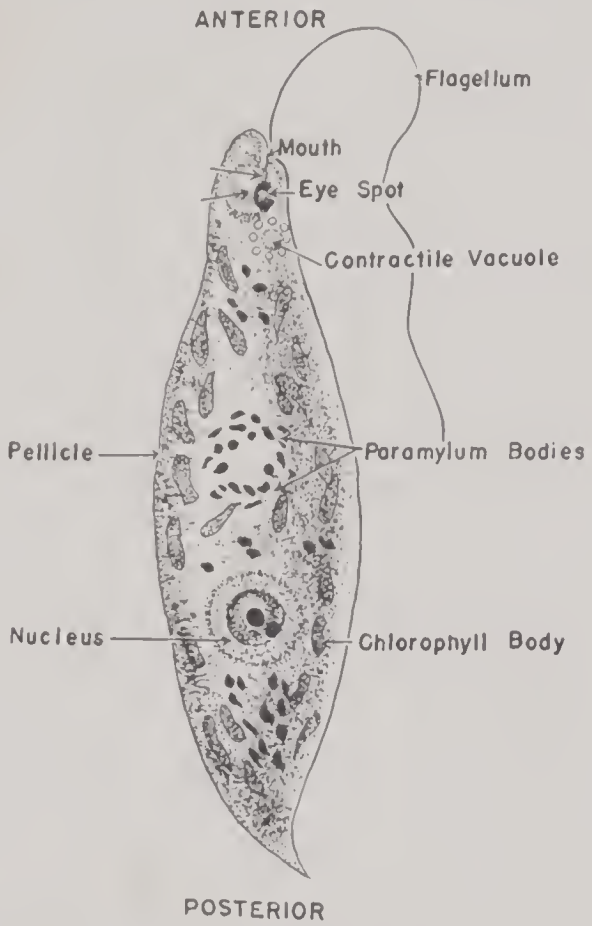


Fig. 45. A typical flagellate, *Euglena*. (Hunter and Hunter: College Zoology.)

along by beating in coordinated rhythm. The motion of the cilia is oblique, revolving the animal as it swims, and the coordination is sufficiently good so that the animal can back up and turn around. All this depends on a system of fine threads that connect rows of granules at the bases of the cilia; if these threads are cut, the coordination is destroyed. Paramecia have two contractile vacuoles, which together can remove a volume of water equal to the total volume of the body within half an hour.* A paramecium has a fixed gullet which ingests food and forms vacuoles, where digestion occurs. Well-fed parameeia reproduce by division two or three times a day, and thus are ideal subjects for studies of the laws governing population growth. Such studies have contributed to an understanding of the growth of human populations.

* In contrast, a man excretes an amount of water equal to his body volume in about three weeks.

A third class of protozoa is the **Sporozoa** (spore formers), which have no special method of locomotion and are parasitic. Malaria, one of the great plagues of mankind, killing some three million people each year, is transmitted by the bite of a mosquito, but is caused by a sporozoan.

The fourth class of protozoa, the **Flagellata,** is named for the long, whiplike protoplasmic projections, called **flagella,** which enable the animals to move. Flagellates are usually more or less oval in shape and have a definite front end from which the flagella project (Fig. 45). Some flagellates, of which the best known is *Volvox*, have taken to living in colonies; they can be seen in pond water as small, hollow green spheres, made of thousands of individual animals, arranged with their flagella outward. The colony, moving by the beating of the flagella, rolls over and over, but keeps one end directed forward. In such a colony there is a beginning of specialization, for the cells at the front have larger light-sensitive spots than the others, and only those in the rear are capable of reproduction. A few flagellates are parasitic; the organism causing African sleeping sickness, which is transmitted by the tsetse fly, is one of these.

III. THE CELLULAR LEVEL OF ORGANIZATION

2. The Porifera or Sponges. The bodies of sponges are organized on the cellular level, so that instead of one cell carrying on all the life activities, as in the protozoa, there is a division of labor, with certain cells specialized to perform particular functions: some cells feed the body, while others support or reproduce it. In the sponge there is cellular differentiation, but little or no cellular coordination to form tissues.

Living sponges resemble a piece of raw liver, and not all of them have a skeleton like that of the bath sponge, which is made of a protein material similar to that of silk and fingernails. Chalk or calcium carbonate forms the skeletal material in some sponges, and silica makes up the skeleton in others called "glass sponges."

These creatures, whose scientific name means "pore-bearer," are actually living filters. They take in water through certain pores, strain out the microscopic organisms which they use for food, and eject the remaining water through other pores (Fig. 46). Certain sponge cells have flagella which beat, creating the current of water necessary for bringing in food and oxygen and for carrying away carbon dioxide and wastes. Each cell of the body is irritable and reacts to stimuli, but there are no sense cells or nerve cells to enable the animal to react as a unified whole. Even the effect of a cut is transmitted only a short distance. Sponges often grow fused together in a single large mass, making it difficult to identify the individual animals.

Sponges are believed to be an evolutionary side line which arose from a different group of protozoa from those which gave rise to the rest of the many-celled animals. There is no evidence to suggest that any of the higher animals evolved from the sponges. Because these organisms are undifferentiated, their classification is difficult, but approximately 3000 species have been described. Most of them are marine forms, although a few species occur in fresh water.

IV. THE TISSUE LEVEL OF ORGANIZATION

3. The Coelenterata. The body of these animals is organized typically as a hollow sac, the interior of which is a digestive cavity opening to the outside by a mouth; hence the name, Coelenterata (coel = hollow; enteron = gut). Coelenterates are believed to have evolved from the same stock as all the higher animals, because, like the latter, they have this central digestive cavity connected to the outside by a mouth (the sponges, in contrast, lack it). The tissues of coelenterates fall into roughly the same categories as do those of higher animals: epithelial,

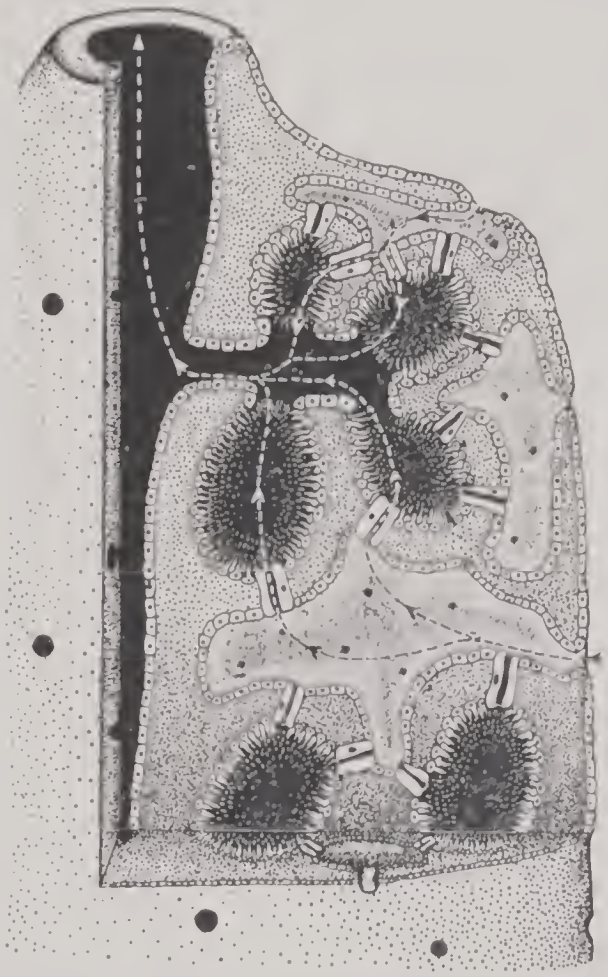


Fig. 46. Diagram of a small section of a typical sponge. The arrows indicate the direction of the flow of water through the pores. (Hunter and Hunter: College Zoology.)

connective, muscular, nervous and reproductive. Although there is considerable division of labor among the cells, they act together in a coordinated way.

The body plan of the coelenterates is typified by a tiny animal, *Hydra*, which lives in ponds and looks to the naked eye like a bit of frayed string (Fig. 47). This animal takes its name from the Greek mythological monster which Hercules fought. You may recall that when the hero cut off one of the Hydra's heads, two more immediately grew in its place. The real hydra has this ability to regenerate, and when it is cut into several pieces, each one grows all the missing parts and becomes a whole animal. The body, which is seldom longer than half an inch, consists of two layers of cells enclosing a central gastrovascular cavity, so called because it performs both digestive and circulatory functions

(Fig. 103). The outer of the two layers of cells in the body wall, the ectoderm, serves as a protective layer; the inner entoderm is primarily a digestive epithelium. The bases of the cells of both layers are elongated into contractile muscle fibers; those of the ectoderm run lengthwise, and those in the entoderm run circularly. By the contraction of one or

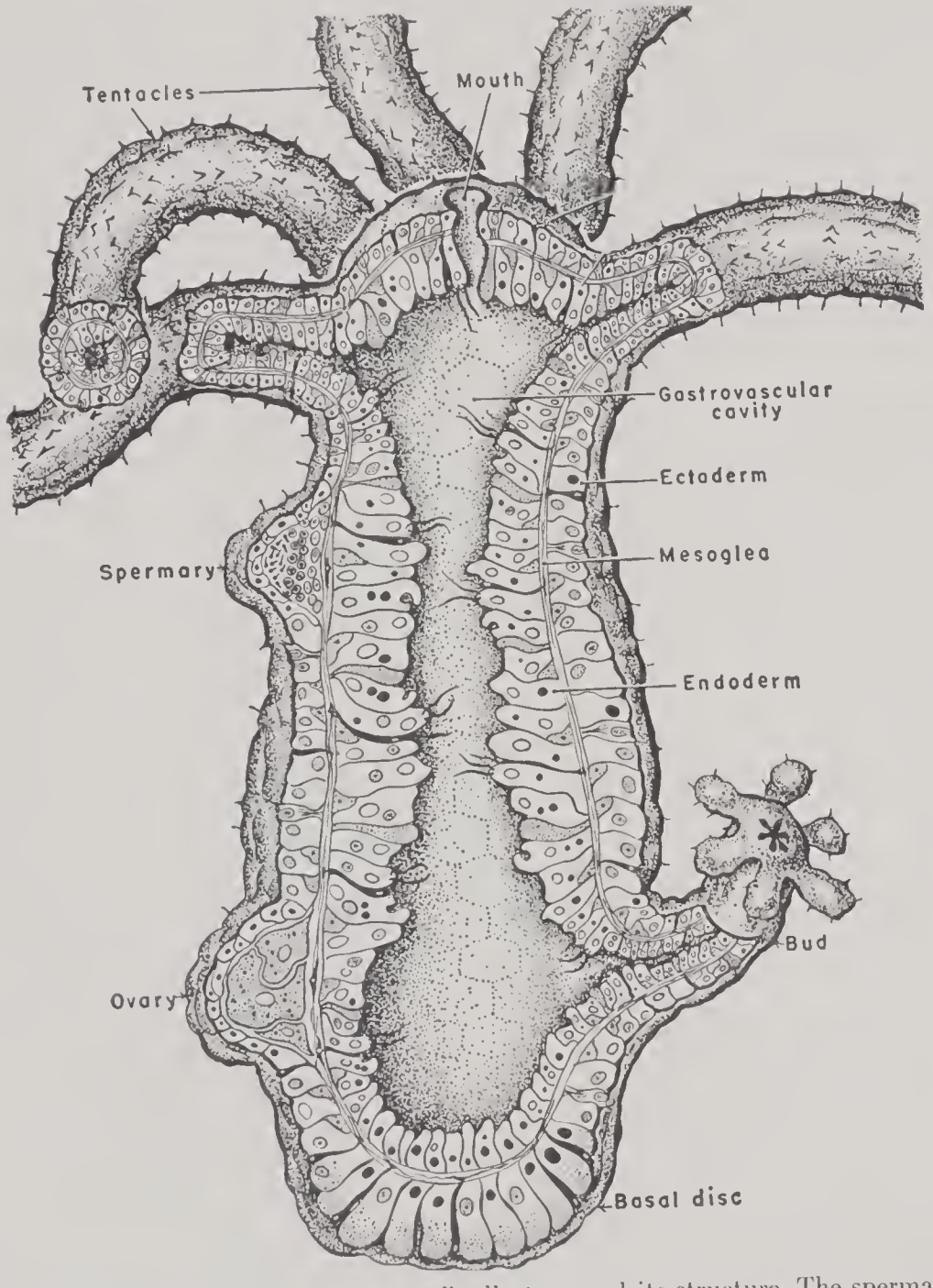


Fig. 47. Diagram of a *Hydra* cut longitudinally to reveal its structure. The spermary and ovary for sexual reproduction are represented on the left, and asexual reproduction by budding is represented on the right. (Hunter and Hunter: College Zoology.)

the other, the hydra can shorten, lengthen or bend its body. Throughout its life the animal lives attached to a rock, twig or leaf by a disc of cells at its base. At the other end is the mouth, connecting the gastrovascular cavity with the outside, and surrounded by a circlet of tentacles, each of which may be as much as one and a half times as long as the body itself. The tentacles, also, are composed of an outer ectoderm and an inner entoderm and may be hollow or solid.

Coelenterates are unique in producing "thread capsules" or **nematocysts,** which lie in the outer layer and which, when stimulated, can release a coiled, hollow thread containing poison to paralyze the small animals upon which it feeds. A nematocyst can be used only once; when it has been discharged, it is discarded and replaced by a new one, produced by special cells. The tentacles encircle the prey and stuff it through the mouth into the gastrovascular cavity, where digestion begins. When the animal has been digested to small fragments, the individual particles are taken up by pseudopods of the entoderm cells, and digestion is completed within food vacuoles in those cells.

Respiration and excretion occur by diffusion, for the body of a hydra is small enough that no cell is far from the surface. The motion of the body, as it stretches and shortens, circulates the contents of the gastrovascular cavity, and some of the entoderm cells have flagella whose beating aids in circulation. The hydra has no other circulatory device.

The first true nerve cells in the animal kingdom are found in the coelenterates. These animals have many nerve cells, which form an irregular network and connect the sensory cells in the body wall with muscle and gland cells. The coordination achieved thereby is of the simplest sort; there is no aggregation of nerve cells to form a "brain" or spinal cord, and an impulse set up in one part of the body goes in all directions more or less equally.

Besides the hydra and hydra-like organisms, the phylum Coelenterata includes such superficially different forms as jellyfish (Fig. 49), corals and sea anemones among its 4500 different species. Both jellyfish and hydroids have bodies composed of an outer ectoderm and inner entoderm, with a nonliving jelly (mesoglea) layer between them; in the hydra, the mesoglea layer is thin, whereas in the jellyfish it is thick and viscous, giving firmness to the body. The fundamental similarity between the two is illustrated in Figure 48, which clearly shows that if a hydra is turned upside down and its mesoglea increased, the result is a jellyfish. The hydra and jellyfish are, then, two ramifications of the same fundamental plan, one adapted for an attached life, the other for a free-swimming life.

Some of the marine coelenterates are remarkable for an alternation of sexual and asexual generations analogous to that in plants. For example, many species of jellyfish reproduce sexually to give rise to hydra-like animals which, in turn, reproduce asexually to form new jellyfishes. Many of the marine coelenterates form colonial organizations of hundreds or thousands of individuals. A colony begins with a single individual that reproduces by budding, but the buds, instead of separating from the parent, remain attached and continue to bud themselves. In time, different types of individuals arise in the same colony, some specialized for feeding, others for reproduction.

The Portuguese man-of-war (*Physalia*, Fig. 49), which superficially looks like a jellyfish, is really a colony of hydroids and jellyfish. The long tentacles of this form are equipped with stinging capsules that can paralyze a large fish and wound a man seriously. The colony is supported by a gas-filled float of vivid, iridescent purplish-green.

The largest known jellyfish, *Cyanea,* may be 12 feet in diameter, and

have tentacles 100 feet long. These orange and blue monsters, among the largest of the invertebrate animals, are a real danger to swimmers in the North Atlantic ocean.

The sea anemones and corals have no jellyfish stage, but occur both as individuals and in colonies. They differ from hydras in that the gastrovascular cavity is divided by a series of vertical partitions into a number of chambers, and the surface ectoderm is turned in at the mouth to line a gullet (Fig. 48). The partitions in the gastrovascular cavity increase the digestive surface, so that an anemone can digest an animal as large as a crab or fish.

In warm shallow seas almost every square foot of the bottom is covered with coral or anemones, most of them brightly colored. The extravagant reefs and atolls of the South Seas are the remains of billions of microscopic, cup-shaped calcareous structures, secreted, during past ages, by coral colonies. Living colonies occur only in the uppermost part of such reefs, adding their own secretions to the mass.

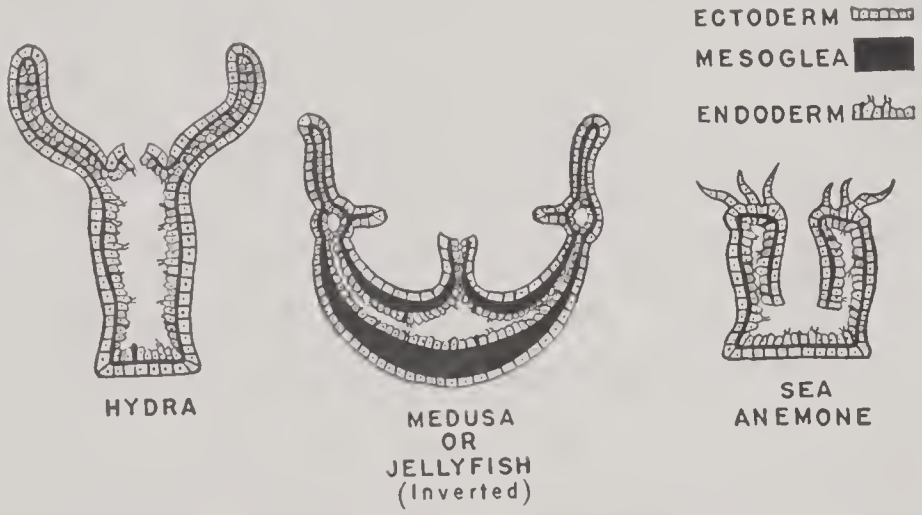


Fig. 48. Comparison of a *Hydra*, an inverted jellyfish, and a sea anemone to show their essential structural similarity. (Hunter and Hunter: College Zoology.)

The **Ctenophores,** whose common names are sea walnuts or comb jellies, are similar in many ways to coelenterates, although they are usually placed in a separate phylum. Their bodies are about the size and shape of an English walnut, and consist of two layers of cells enclosing a mass of jelly; the outer surface is covered with eight rows of cilia, like combs, by which the animal moves through the water (Fig. 50). At the upper pole of the body is a sense organ, containing a mass of limestone particles and balanced on four tufts of cilia connected to sense cells. When the body turns, these particles bear more heavily on the lower cilia, stimulating the sense cells, which cause the cilia to beat faster and bring the body back to its normal position. Nerve fibers running from the sense organ to the cilia control the beating, and if they are cut, the beating of the cilia below the incision is disorganized. Ctenophores differ from coelenterates in lacking stinging capsules and in having only two branched tentacles instead of many.

V. THE ORGAN LEVEL OF ORGANIZATION

4. The Platyhelminthes or Flatworms. An advance over the coelenterate, tissue level of organization is demonstrated by the free-living

flatworms, such as *Planaria*, which, though less than an inch long, have definite organs. Flatworms live in both fresh and salt water, creeping

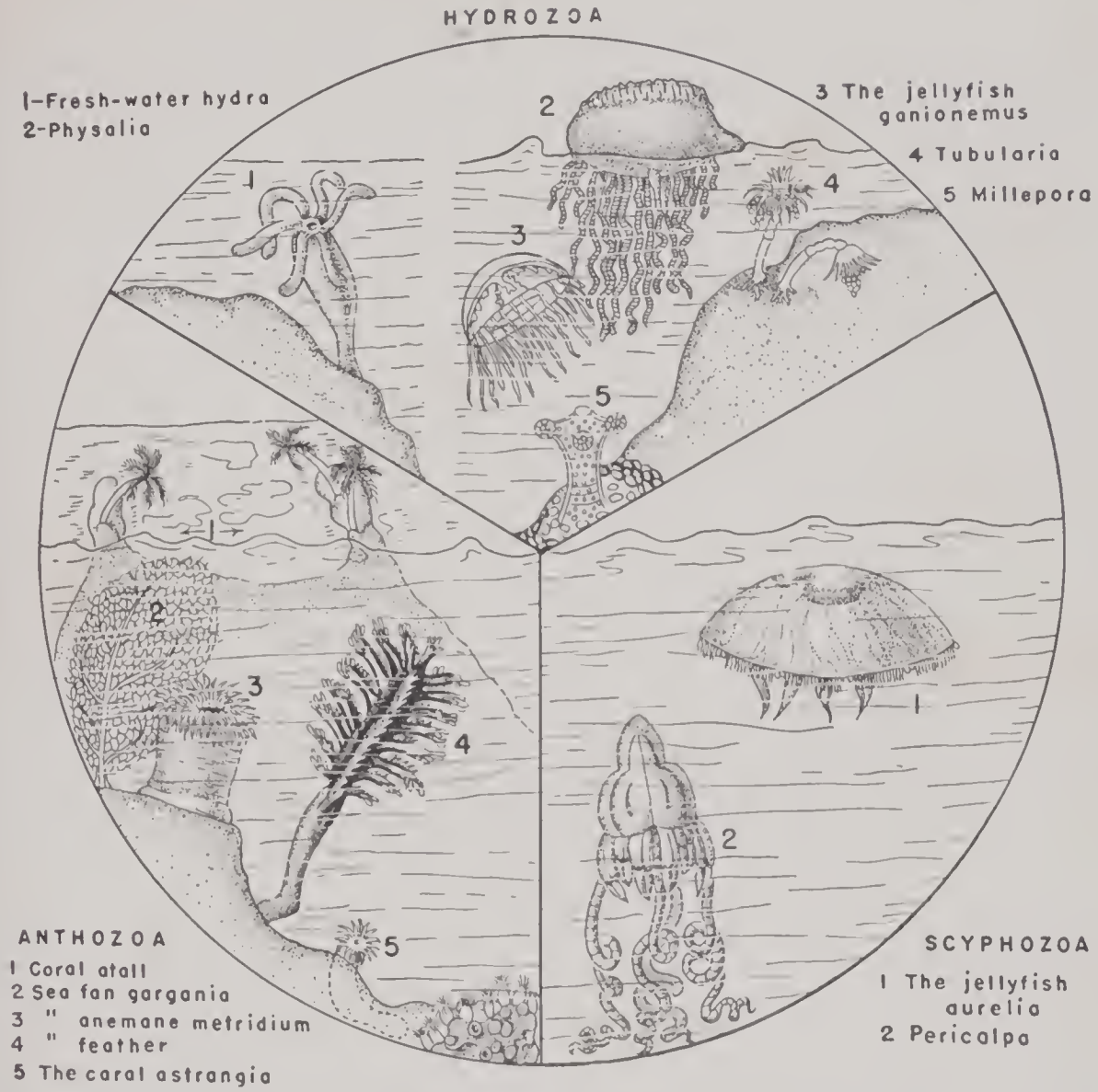


Fig. 49. Some common representatives of the phylum Coelenterata, grouped by classes. (Hunter and Hunter: College Zoology.)

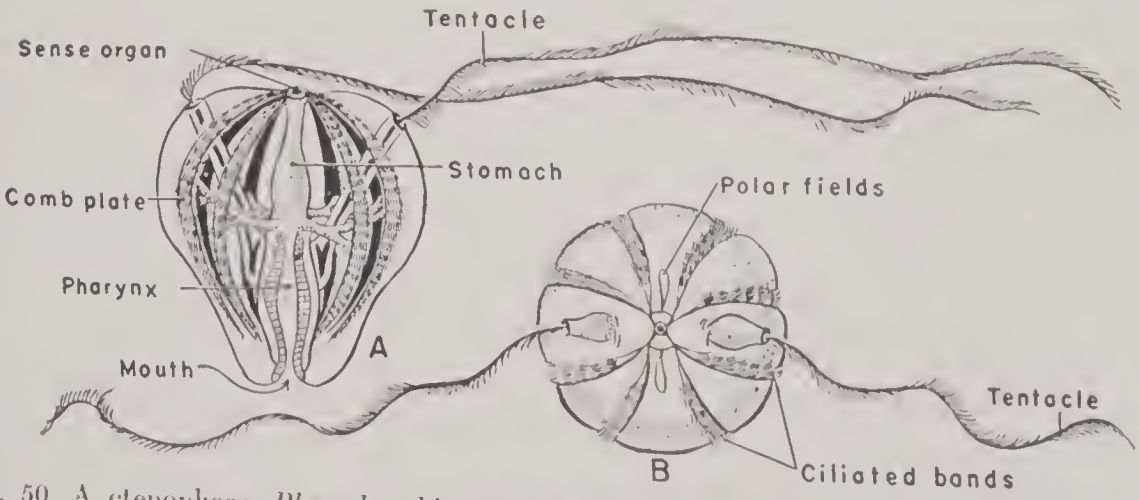


Fig. 50. A ctenophore, *Pleurobrachia*. *A*, Side view; *B*, top view. (Hunter and Hunter: College Zoology.)

over rocks, debris and leaves. Like the hydra, flatworms have a single gastrovascular cavity (Fig. 103)—sometimes extensively branched—

connected to the outside by a single opening, the mouth, which is on the middle of the ventral surface. In addition to an outer ectoderm and an inner entoderm, the flatworm has a third, middle layer, called the mesoderm, which comprises most of the body and forms many of the organs. There are several simple organs—a muscular pharynx for taking in food, eyespots and other sense organs on the head, and complex reproductive organs. The worm has a definite anterior and posterior end, and keeps one surface (the back or dorsal one) always upward as it crawls along. Locomotion is achieved partly by means of cilia on its under or ventral surface, and partly by muscular contractions, similar to those of the earthworm. Gland cells on the ventral surface secrete a slime which facilitates movement.

Flatworms can survive without food for months, gradually digesting their own tissues and growing smaller as time passes. As in the coelenterates, respiration takes place by diffusion. In order to secrete waste products, the flatworm has an organ not found in lower forms. This structure, which is formed from the mesoderm, consists of a network of fine tubes opening to the surface by pores, and ending in branches known as **flame cells** (Fig. 114). Each of the latter is a single, hollow cell containing a tuft of cilia which, in beating, resembles a flame. The motion of the cilia drives the excreted fluid along the tubes and out the pores. *Planaria,* which lives in fresh water, has the same problem of getting rid of excess water faced by the fresh-water protozoa, and the flame cells, like the contractile vacuole, solve it. Some flatworms have an interesting mechanism for defense: from the hydras they eat, they confiscate, intact, the stinging capsules, which become part of their own epithelium and are used in the appropriate manner.

Besides the free-living flatworms like *Planaria,* there are two groups of parasitic ones, the **Trematoda,** or flukes, and the **Cestoda,** or tapeworms. Parasitism has been defined as a relationship between two animals in which one lives on or in the other, at its expense. Such a relationship usually evolves gradually. In the beginning, two species may simply live together habitually, one of the species deriving benefit from the association, and the other remaining unharmed by it—the relationship known as **commensalism.** This is probably the first step toward parasitism. Some flatworms live attached to the gills of the king crab and get their food from scraps of the crab's meals. They receive shelter and transportation from their host, but apparently do not injure it in any way. When both species receive benefit from the association, the relationship is called **mutualism,** exemplified by the alga-fungus relation in lichens (p. 65), and by the termites and their intestinal flagellates (p. 208). The relationship of parasitism begins when one of the two species involved begins to harm the other by depriving it of necessary food, or by living on its tissues, thus causing disease.

The flukes are structurally like the free-living flatworms, but differ in having one or more suckers* with which to cling to the host, and a thick outer layer, the cuticle, in place of cilia. The organs of digestion, excretion and coordination are like those of the other flatworms, but the

* Leeches, which also have suckers, are not flukes, but more highly organized animals related to earthworms.

reproductive organs are extremely complex. The flukes parasitic on human beings are the blood flukes, widespread in China, Japan and Egypt, and the liver flukes, common in China, Japan and Korea. Both these parasites go through complicated life cycles, involving a number of different forms, alternation of sexual and asexual generations, and parasitism on one or more intermediate hosts such as snails and fishes.

Tapeworms are long, flat, ribbon-like animals, some species of which live as adults in the intestines of probably every kind of vertebrate, including man. The head end of a tapeworm (Fig. 196) is equipped with suckers and often has a circle of hooks by means of which it attaches to the lining of the intestine. Behind the head is a growing region which constantly gives rise to new body sections by budding. The rest of the body consists of a series of these sections. Tapeworms have no mouth and no trace of a digestive system; they live by soaking up the digested materials present in the intestine of their host (p. 408).

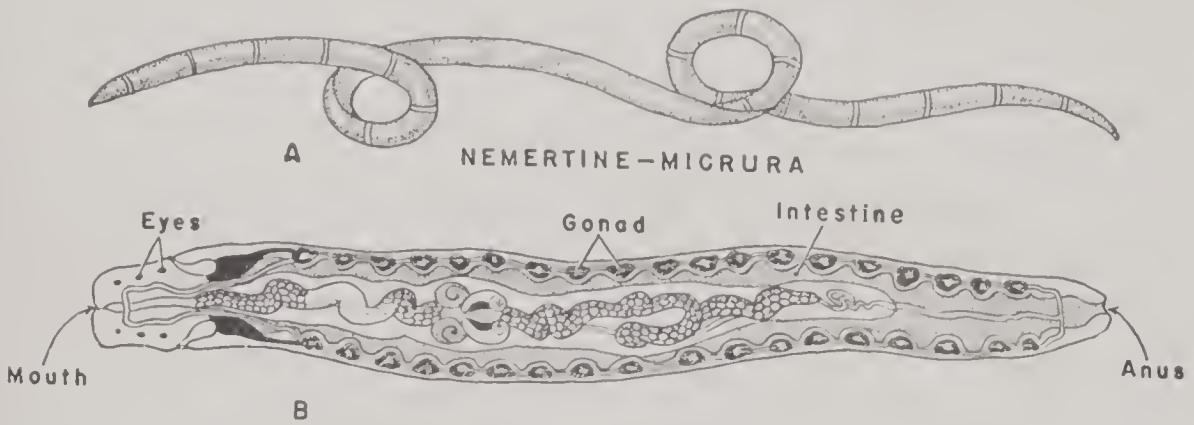


Fig. 51. A typical proboscis worm or nemertean. *A*, External appearance. Note the colored bands which are present on many species. *B*, Diagram of the internal anatomy. Note the three longitudinal blood vessels (white) and the digestive system composed of mouth, intestine and anus. (Hunter and Hunter: College Zoology.)

VI. THE ORGAN SYSTEM LEVEL OF ORGANIZATION

5. The Nemertea or Proboscis Worms. This group of animals is important to us only as an evolutionary landmark, for the proboscis worms are the simplest living animals which illustrate the organ system level of organization (Fig. 51). None of them is parasitic; hence they are harmless to man and other animals; and none is of economic importance. Almost all of them are marine, although a few inhabit fresh water or damp soil. They have long narrow bodies, either cylindrical or flattened, varying in length from an inch to 60 feet. Some of them are a vivid orange, red or green with black or colored stripes. Their most remarkable organ—the proboscis, from which they take their name—is a long, hollow, muscular tube which they evert from the anterior end of the body and use for seizing food. The proboscis secretes mucus, helpful in catching and retaining the prey. Some species have a hard point at the tip of the proboscis for wounding the enemy, and poison-secreting glands at the base of this point. The proboscis is thrust outward by the pressure of the surrounding muscular walls on the contained fluid; a separate muscle inside the proboscis retracts it.

The important advances displayed by the nemerteans are, first, a

complete digestive tract, with a mouth at one end for taking in food, an anus at the other, for eliminating feces, and an esophagus and intestine in between. This is in contrast to the coelenterates and planarians, whose food enters, and wastes leave, by the same opening. In the proboscis worm metabolic wastes are eliminated from the body by flame cells, as they are in the flatworms. A second advance exhibited by the nemerteans is the separation of digestive and circulatory functions. These animals are the most primitive organisms to have a separate circulatory system. It is, of course, rudimentary, consisting simply of three muscular tubes—the blood vessels—which run the length of the body and are connected by transverse vessels. Surprisingly, these primitive forms have red blood cells filled with hemoglobin, the same red pigment which transports oxygen in human blood. Nemerteans have no heart, and the blood is circulated through the vessels by the movements of the body. The nervous system is more highly developed than it is in the flatworm; there is a "brain"* at the anterior end of the body, consisting of two groups of nerve cells (ganglia), connected by a ring of nerves extending around the sheath of the proboscis, and two or three nerve cords extending the length of the body.

The phylum **Nematoda,** made up of round worms, has a great many members (about 8000 species), all of them remarkably similar in general body pattern. Some live in the sea, others in fresh water, in the soil, or in other plants or animals as parasites. About fifty species are human parasites, of which the most detrimental are the hookworm, trichina worm (Fig. 197), ascaris worm, filaria worm and guinea worm. A microscopic examination of a shovelful of earth from almost anywhere in the world will reveal a number of tiny white worms which thrash around, coiling and uncoiling. Their long, cylindrical bodies, pointed at both ends, are covered with a tough cuticle layer. In contrast to the nemerteans, which have cilia all over the epithelium and the lining of the digestive tract, none of the nematodes has any cilia at all.

With the evolution of a complete digestive system, a separate circulatory system, and a nervous system composed of a "brain" and nerve cords, as illustrated in the proboscis worm, the essential structures of higher animals were established. The proboscis worm is not believed to be the actual ancestor of the higher forms, but is thought to be like the now extinct ancestor common to both the higher animals and itself. Evolution beyond this point branched out in a great many different directions, and the more advanced animals cannot be arranged in a single series of progressively higher and more complex forms. One main branch of evolution led to the vertebrates, another to the insects and other arthropods; and another to the clams, squids and other molluses. Besides these familiar forms, there are others, belonging to different evolutionary branches, about which, since they neither serve nor menace us, we think little. One frequently hears people ask of such animals,

* The word "brain" is loosely applied to the aggregation of nerve cells at the anterior end of the nerve cord, which acts as a reflex center. It should not be inferred that anything like thought processes occurs in any of the lower animals.

"What good are they?" The answer is that, since the various forms of life do not exist to serve man, it would be quite as reasonable to ask what good we are to them.

6. The Rotifera. Some of the more obscure animals just mentioned make up the phylum Rotifera (wheel animals). These aquatic, microscopic worms, although no larger than many of the protozoa, have many-celled bodies with a complete digestive tract; an excretory system made up of flame cells and a bladder; a nervous system with a "brain" and sense organs; and a characteristic crown of cilia on the head end which gives the appearance of a spinning wheel.

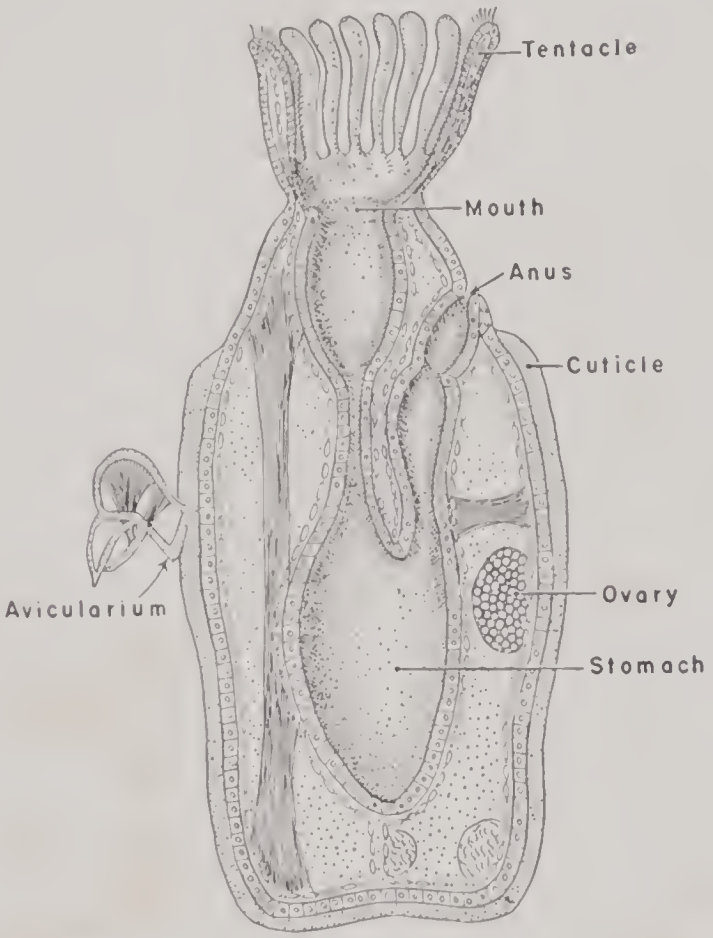


Fig. 52. A bryozoan, *Bugula*, cut open longitudinally to reveal its internal structure. (After Curtis and Guthrie, Hunter and Hunter: College Zoology.)

7. The Gastrotricha. This is another phylum of microscopic, aquatic worms which are like rotifers in many respects, but have no crown of cilia. Some of the fresh-water gastrotrichs are peculiar in that they apparently consist entirely of females which reproduce by parthenogenesis; no males of this group have ever been found.

8. The Bryozoa. The Bryozoa, or moss animals, live in colonies that superficially resemble those of the coelenterates (Fig. 52). The colonies of some species, delicately branched and beautiful, are sometimes mistaken for seaweed; other species form colonies which appear as thin, lacy incrustations on rocks. Each animal secretes about itself a vase-shaped protective case of calcium carbonate or of a horny, protein material, into which it can withdraw when danger threatens. Around the animal's mouth is a circular or horseshoe-shaped ridge, called a lophophore ,with a set of ciliated tentacles. An adaptation to living in a "vase" is the U-shaped digestive system. In one class the anus is just

outside the ring of tentacles; in another it lies immediately inside. New members of the colony arise by budding from the older ones, and new colonies arise as the result of sexual reproduction during certain seasons.

Any bryozoan colony also has specialized members, called **avicularia,** which resemble the head of a bird. These organisms are in constant motion from side to side, and, as they move, a peculiar organ, shaped like a bird's lower beak and operated by muscles, frequently snaps open and shut. The purpose of the avicularia is not to catch food—other members do that—but to keep small animals from settling on the colony.

9. The Brachiopoda. This is another phylum characterized by a lophophore. The animals are commonly known as lampshells and superficially resemble a clam. Like the latter, they have two shells, usually calcareous, that can be opened and closed by muscles. But unlike the clam, whose two shells are on the right and left sides of the body, the brachiopod shells lie above and below it, the bottom shell being attached to a rock or other object by a sturdy, muscular stalk. All brachiopods live in the sea. Although only about 200 species of this extremely ancient phylum exist today, there once were more than 3000 species. Because of their great age and well-preserved hard shells, the fossil brachiopods are useful to geologists in determining the age of rocks. Fossils obtained from rocks more than 500,000,000 years old are almost exactly like the brachiopods living today.

Some of the less familiar invertebrates—the Bryozoa, Brachiopoda and Phoronida—as well as all the others to be discussed presently, are characterized by a body cavity or **celom,** lying between the body wall and the wall of the digestive tract. This cavity arises during embryonic development from a split in the mesoderm layer, and hence is lined with mesoderm. The development of the celom, which freed the digestive tract from the body wall, and permitted the two sets of muscles to contract independently, was an important step toward the development of the higher animals.

10. The Annelida. Among the most familiar invertebrate animals are the earthworms, members of the phylum Annelida (Fig. 53). This word, which means "ringed," refers to the fact that the body of the worm is made of a series of rings or segments. Both the internal organs and the body wall are segmented, so that every animal consists of a series of a hundred or more similar units, each of which contains one or a pair of organs of each system. The segments are separated from each other by transverse, bulkhead-like partitions. The chief evolutionary advance shown by the earthworms over the lower forms is this development of segmentation, for each segment constitutes a subunit of the body that may be specialized to carry on a particular function. The dividing of the body into segments is thus similar, on a larger scale, to the original division of the animal body into cells to provide for local specialization. In the earthworm the individual segments are almost all alike, but in many of the other segmented animals—the arthropods and chordates—the specialization of different segments reaches a point where the segmentation of the body plan is obscured.

The eelom, or body cavity, of the annelids is large and well developed, and the entire body consists essentially of two tubes, one within the other. The outer tube is the body wall, and the inner tube, the wall of the digestive tract. The eelom is filled with a fluid which bathes the internal organs and is an intermediate, in transporting gases, food and wastes, between the circulatory system and the individual cells of the body.

The digestive system of the earthworm shows several advances over that of the proboscis worm: there is a muscular pharynx for swallowing food, an esophagus, and a stomach of two parts—a thin-walled **crop,** where food is stored, and behind it, a thick-walled muscular **gizzard,** where it is ground to bits. The rest of the digestive system is a long, straight intestine, where digestion and absorption take place, terminating in an anus which opens to the outside at the posterior end.

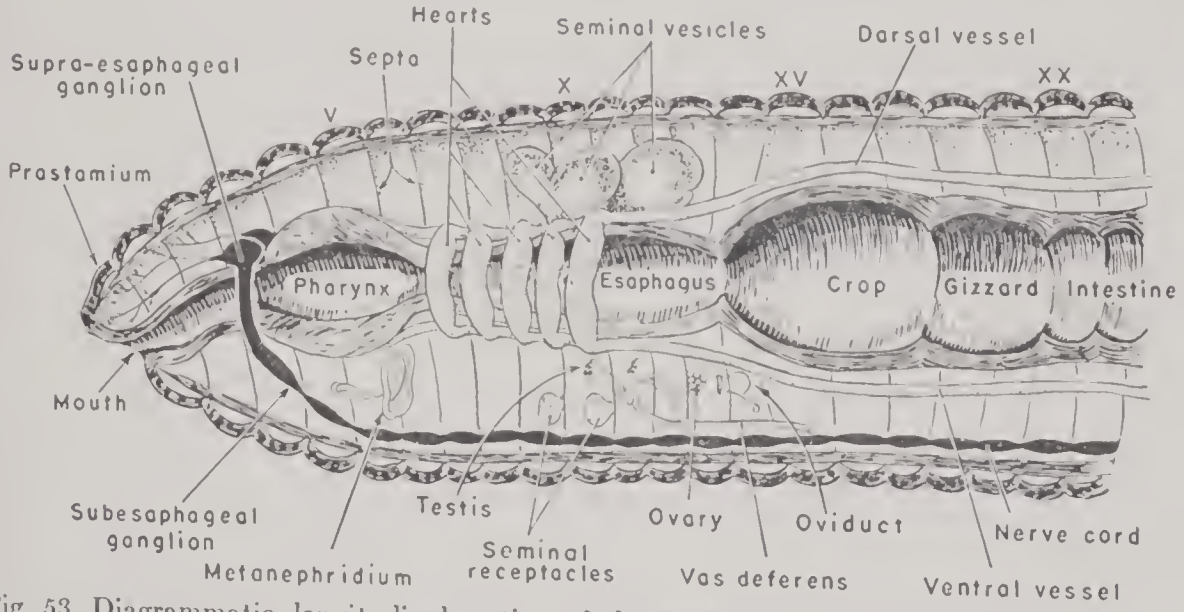


Fig. 53. Diagrammatic, longitudinal section of the anterior part of an earthworm, showing internal structures. (Hunter and Hunter: College Zoology.)

The circulatory system is also marked by advances in complexity and efficiency over that of the primitive proboscis worm. In the earthworm it consists of two main vessels: one lies just dorsal to the digestive tract, collects blood from numerous segmental vessels, and, being contractile, pumps the blood anteriorly; the other, in which blood flows posteriorly, lies just below the digestive tract, and distributes blood to the various organs. In the region of the esophagus the dorsal and ventral vessels are connected by five pairs of muscular tubes, called "hearts," which propel the blood to the ventral vessel. There are also smaller lateral and ventral distributing vessels, and tiny capillaries in all the organs as well as in the body wall.

The excretory system is composed of paired organs repeated in almost every segment of the body. Each individual organ, called a **nephridium,** consists of a ciliated funnel, opening into the eelomic cavity, and connected by a tube to the outside of the body (Fig. 115). Wastes are removed from the eelomic cavity partly by the beating of the cilia and partly by currents set up by the contraction of muscles in the body wall. The tube of the excretory organ is surrounded by a capillary net-

work, so that wastes are removed from the blood stream as well as from the eelomic cavity.

The nervous system, too, is more advanced than that of the proboscis worm, for it consists of a large, two-lobed aggregation of nerve cells located just above the pharynx, and another ganglion just below the pharynx; around the latter organ is a ring of nerves which connects the two ganglia. From the lower ganglion a nerve cord (actually, two closely united cords) extends the entire length of the body, beneath the digestive tract. In each segment there is a swelling of the nerve cord, a segmental ganglion, from which nerves extend laterally to the muscles and organs of that segment. The segmental ganglia coordinate the contraction of the muscles of the body wall, so that the worm can creep along. The nerve cord contains certain large nerve fibers which transmit nerve impulses more rapidly than ordinary fibers, and which, when danger threatens, stimulate the muscles to contract and draw the worm back into its burrow. Living a subterranean life, the earthworm has no well-developed sense organs, but some of its sea-dwelling relatives, such as the sandworm, or *Nereis*, have two pairs of eyes, and other organs sensitive to touch and to chemicals in the water.

Besides serving as bait and as food for birds, earthworms are of great service to man in turning over the soil. By making it more porous, thus allowing air to penetrate freely and water to drain properly, they facilitate the growth of roots and hence increase the agricultural yield. In their burrowings through the earth the worms swallow bits of soil, grind them to smaller bits, and discharge them above the surface, well mixed with organic matter. The amount of earth moved in this way is remarkable; it is calculated that every ten years earthworms turn over enough soil to form a layer 2 inches thick over the entire land surface of the world.

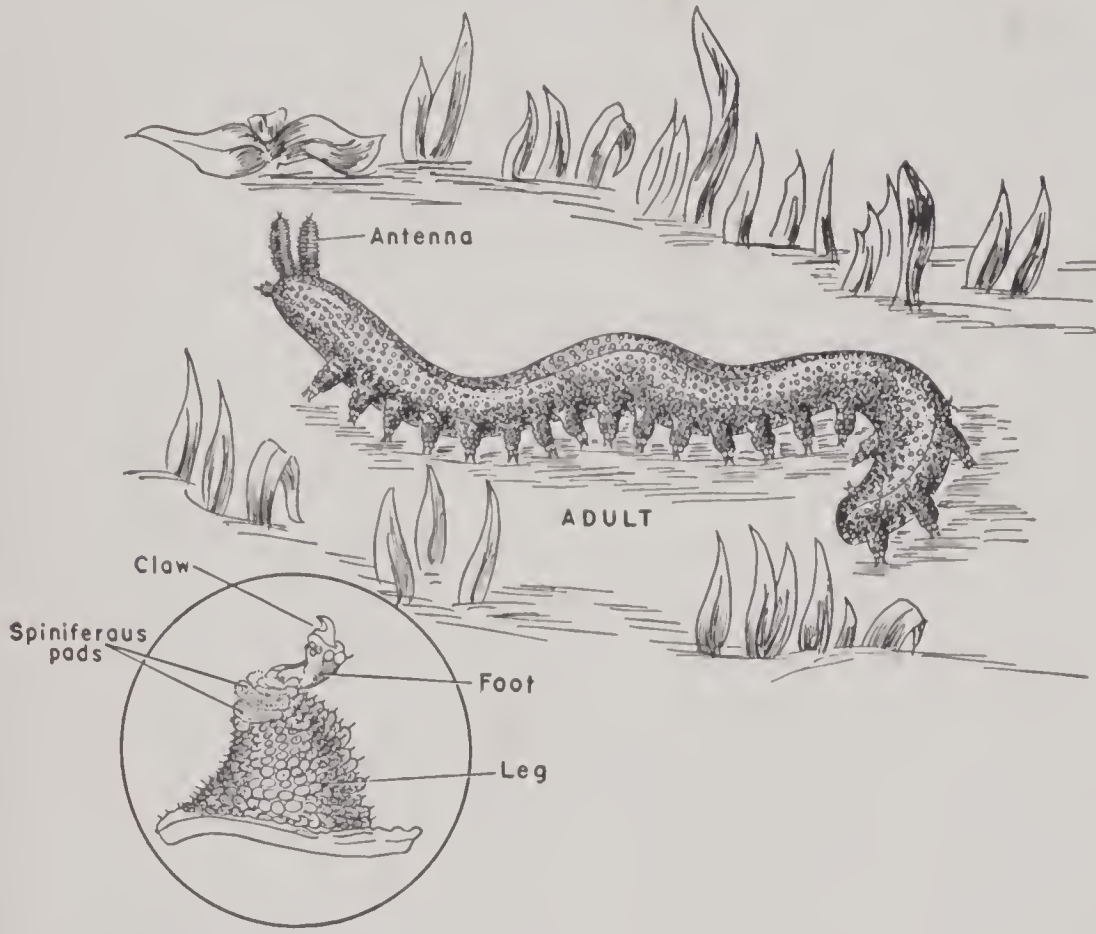
Earthworms are not the only members of their phylum; it contains some 8000 species divided into four classes. One of these is the **Polychaeta** (many bristles), made up of marine worms which swim freely in the sea, burrow in the sand and mud near shore, or live in tubes formed by secretions from the body wall. Each segment of their bodies has a pair of bristled paddles extending laterally.

The members of the class **Oligochaeta** (to which the earthworm belongs) are characterized, as their name indicates, by having few bristles per segment.

The **Archiannelida** (primitive annelids) are a small group of simple worms which are not segmented externally and do not have bristles.

The fourth class of annelids is the **Hirudinea,** made up exclusively of leeches. These worms are provided with stout muscular suckers at the anterior and posterior ends for clinging to their prey. Most leeches feed by sucking the blood of vertebrates; they attach themselves by their suckers, bite through the skin of the host, and suck out a quantity of blood, which is stored in pouches in the digestive tract. Their meals may be infrequent, but they can store enough food from one meal to last a long time. The so-called "medicinal leech" is a fresh-water worm about 4 inches long which physicians used for blood-letting when the humoral theory of disease was in vogue.

It is generally believed that the annelids and arthropods developed from a common ancestral line, a theory substantiated by the existence of a curious animal called **peripatus** (Fig. 54), which lives in the moist, tropical forests of Africa, Australia, Asia and South America. This caterpillar-like creature, 2 or 3 inches in length, appears to be a connecting link between the two phyla. It is not believed, however, to be the ancestor of the present-day arthropods, but rather, a descendent which has not changed much from the original ancestor of both annelids and arthropods, for its anatomy is a mixture of the characteristics of both. It has many pairs of legs, each of which has a pair of claws at the tip.



LEG SHOWING ARTHROPOD–LIKE CLAWS

Fig. 54. Peripatus, a member of the Onychophora, a so-called missing link between the Annelida and the Arthropoda. *Inset,* An enlarged view of a leg of peripatus, showing the arthropod-like claws at the end. (Hunter and Hunter: College Zoology.)

Its excretory, reproductive and nervous systems are similar to those of annelids, but its circulatory system is like that of arthropods, as is its respiratory system, which consists of air tubes (tracheal tubes). Some zoologists classify the peripatus as a separate phylum (Onychophora); others classify it with the annelids; and still others place it with the arthropods.

11. The Arthropoda. The animals which make up this phylum are, without doubt, the most successful, biologically, of all animals, for there are more of them (about 650,000 species are known, of which some 600,000 are insects), they live in a greater variety of habitats, and can eat a greater variety of food than the members of any other phylum. There are five classes of arthropods: the **Crustacea** (Fig. 55), including

crabs, lobsters, shrimps, barnacles, water fleas and many other marine and fresh-water forms; the **Centipedes** (Fig. 56), which are fast-moving carnivorous forms, some of which can inflict a painful bite; the **Millipedes,** which are slower-moving plant-eaters; the **Arachnids,** including spiders, scorpions, ticks and mites; and the **Insects** (Fig. 57).

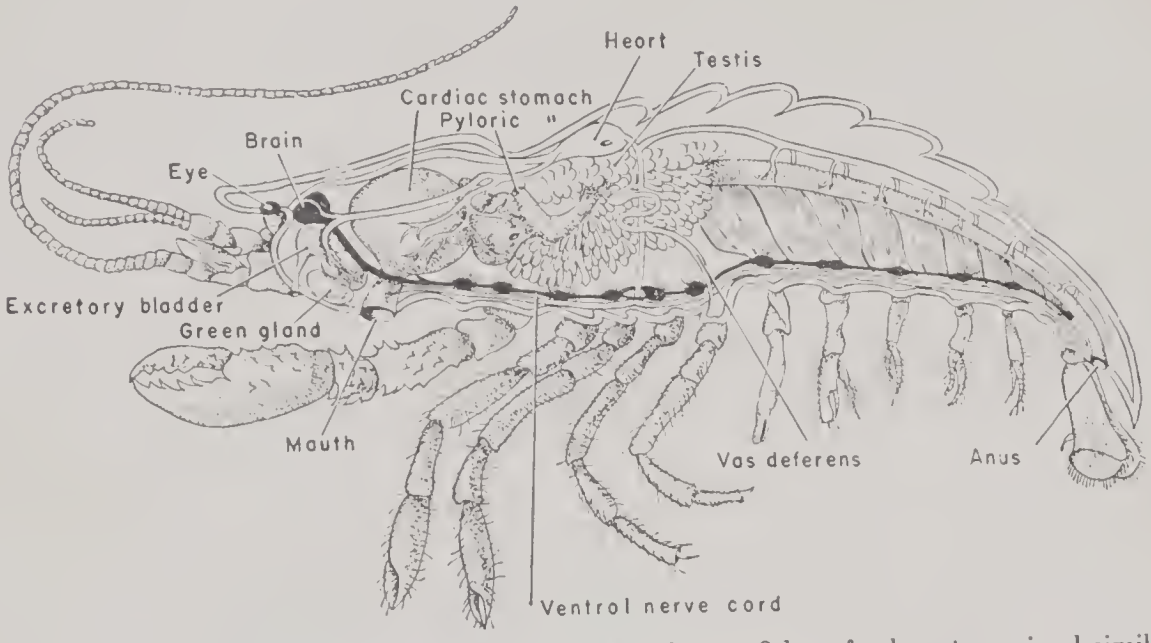


Fig. 55. Diagrammatic, longitudinal section of a male crayfish, a fresh-water animal similar to a lobster. (Hunter and Hunter: College Zoology.)

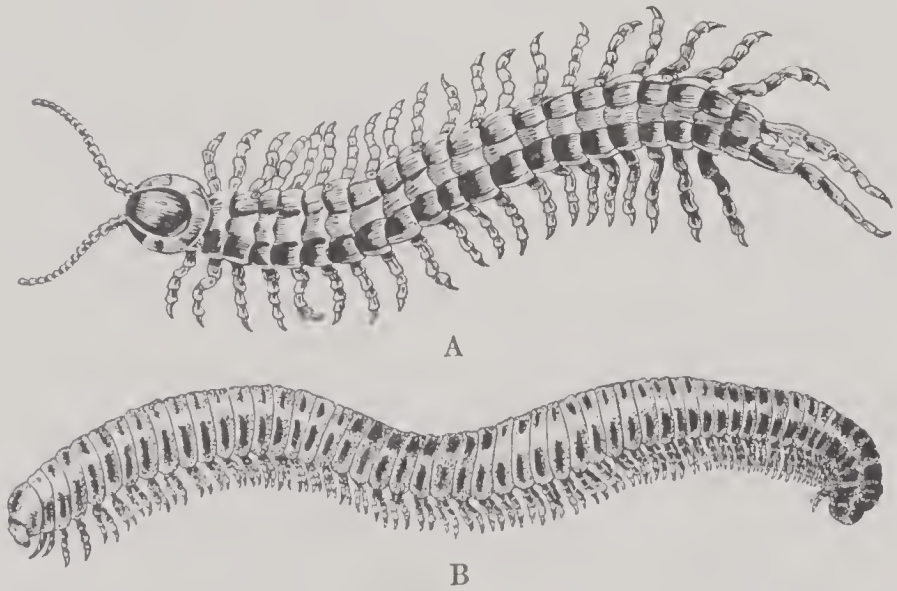


Fig. 56. *A*, Centipede, a member of the class Chilopoda. Centipedes have one pair of appendages per segment. *B*, Millipede, a member of the class Diplopoda. Millipedes have two pairs of appendages per segment. (After Koch; from Hunter and Hunter: College Zoology.)

The word "arthropod" has reference to the paired, jointed appendages characteristic of these animals which are used in a variety of ways: as swimming paddles, walking legs, mouth parts, or accessory reproductive organs for transferring sperm. Besides being segmented, arthropods have in common a hard external coat of cuticle secreted by the underlying epithelium. The cuticle has an outer, waterproof, waxy layer, a rigid, middle layer, and a flexible, inner layer of chitin. The rigid layer is thin in certain regions, such as the joints of the legs and between the body

segments, allowing the cuticle to be bent. Such a layer protects the body from excessive loss of moisture and from enemy attack, and gives necessary support to the underlying soft tissues. But it has disadvantages,

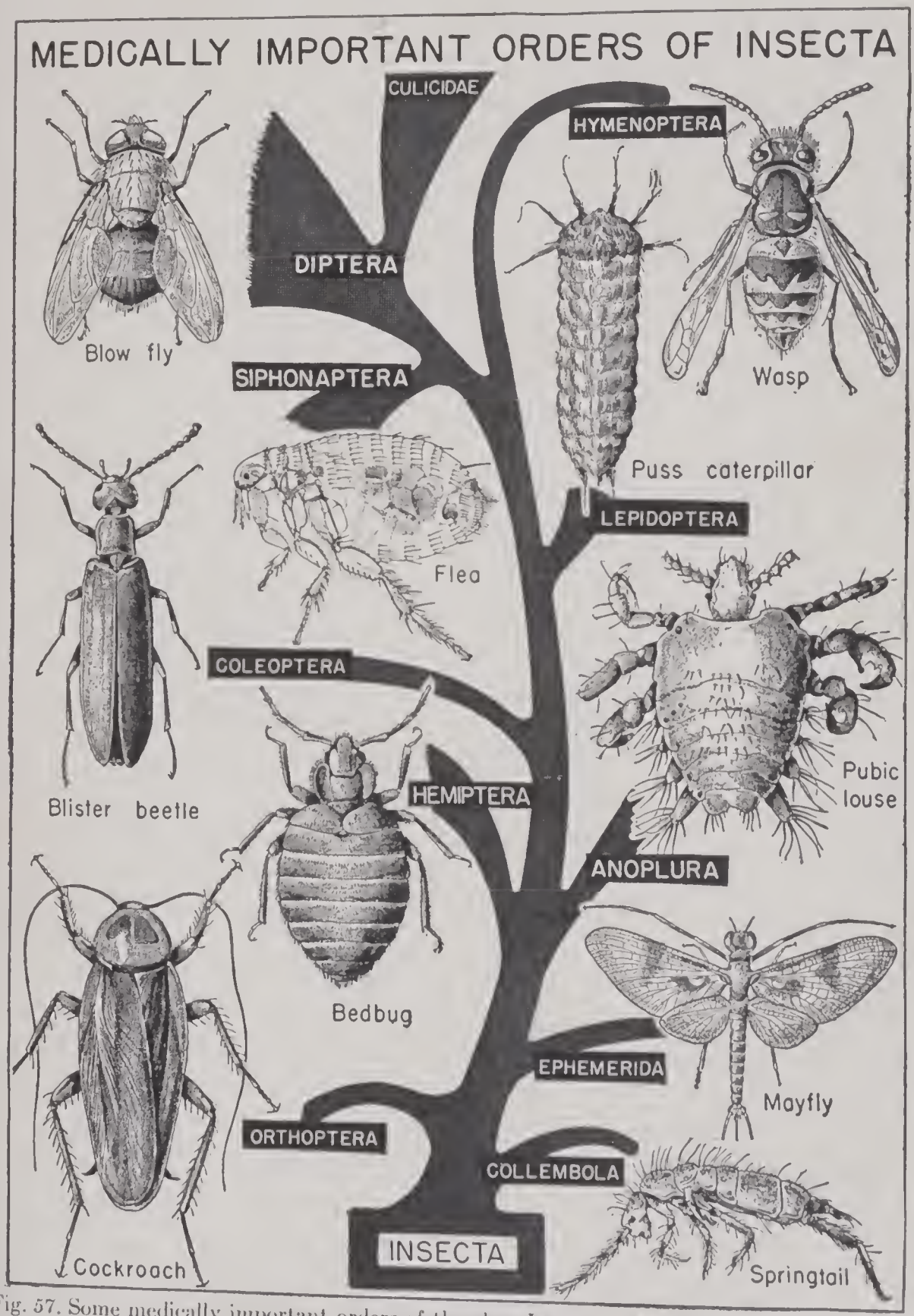


Fig. 57. Some medically important orders of the class Insecta. (Mackie, Hunter and Worth: Manual of Tropical Medicine.)

too: body movement is somewhat restricted, and, in order to grow, the arthropod must shed the outer shell periodically, and grow another, larger one, a process which leaves him temporarily vulnerable.

The bodies of most arthropods are divided into three regions: the **head,** always composed of exactly six segments, the **thorax,** and the **abdomen,** both of which are composed of a variable number of segments. In contrast to most annelids, each arthropod has a fixed number of segments which remains the same throughout life. We cannot begin to describe all the variations in body plan and in the shape of the jointed appendages in the numerous species. The nervous system of the more primitive arthropods is like that of the annelids, but in the higher ones the successive ganglia usually fuse together. The arthropods have a variety of well-developed sense organs: complicated eyes, such as the compound eyes of insects; organs located in the antennas, which are sensitive to touch and to chemicals; organs of hearing; and touch cells on the surface of the body. The true celom is small and is made up chiefly of the cavities of the reproductive system; the large body cavity is not a celom, but a blood cavity—part of the circulatory system—for the latter includes, besides the enclosed vessels, open spaces throughout the body by means of which the organs are bathed. There is a pumping organ, or "heart," in the dorsal part of the body which stirs the blood around in these spaces. Most of the aquatic arthropods have a system of gills for respiration, whereas the land forms usually have a system of fine, branching air tubes or tracheas, which conduct air to the internal organs. The digestive system, typically, is a simple tube like that of the earthworm, lined in part with a cuticle similar to the outer covering of the body. In insects and some other forms the excretory system consists of tubules which empty into the digestive tube. These metabolic wastes then pass out of the body with the feces, through the anus.

Insects are the only invertebrates to have developed wings (though not all species have done so), but these structures are analogous only, not homologous, to the wings of the vertebrates. Insect wings usually occur in two pairs; the exception to this are the wings of flies, which occur as one pair, plus a pair of balancers—the remains of the second original pair. In most insects both sets of wings are functional as flying organs, but in grasshoppers and beetles the anterior pair are simply stiffened protective devices for the functional posterior pair.

In some insect species, individuals are differentiated into a number of types, a kind of organization rather like that of the coelenterate or bryozoan colony. But the members of an insect colony are not joined together anatomically as are these lower forms; they constitute a **social colony.** A termite colony, for example, contains "reproductives"—the king and queen—which give rise to all the other members of the colony; "soldiers," which protect the colony from enemies; and "workers," which gather food, build the nest and care for the young. Both soldiers and workers are sterile, and neither reproductives nor soldiers can feed themselves. Thus the members of the colony are completely dependent on each other. Each year new reproductives develop in a colony as winged forms, which leave the group, mate, and form a new colony.

The behavior of termites and other insects is guided to a remarkable extent by **instincts,** which are unlearned patterns of behavior present from birth. For example, the workers which hatch from the eggs laid by

a queen termite build a nest for her exactly like the ones built by other members of the species, although they have no model to copy, and, presumably, they cannot learn from the queen how her original nest was constructed.

12. The Mollusca. This phylum, with its 80,000 species, is the second largest of all the animal phyla. It includes the oysters, clams, octopuses, snails, slugs, and the largest of all the invertebrates—the giant squid, which achieves a length of 50 feet, has a circumference of 20 feet, and weighs several tons.

The adult body plan of these animals is quite different from that of any other group of invertebrates, but the more primitive molluscs have a characteristic larval form, called a **trochophore,** similar to the larval form of certain marine annelids. This suggests that the molluscs and

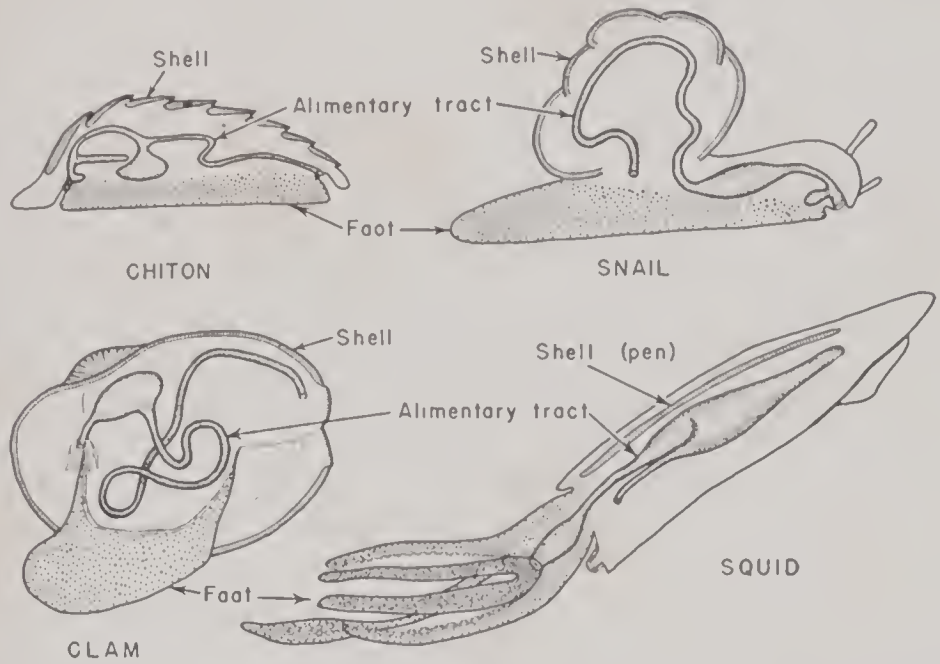


Fig. 58. Variations of the basic molluscan body plan in chitons, snails, clams and squids. Note how the shell, foot and alimentary canal have changed their positions in the evolution of the different groups. (Modified after Buchsbaum; Hunter and Hunter: College Zoology.)

worms arose from a common ancestral type; the worms, however, evolved a segmented body plan, while the molluscs evolved a unique body plan without segmentation. The sluggish marine animal, the **chiton** (Fig. 58), which lives by scraping algae off the rocks of the seashore, is probably closest to the ancestral molluscan type. Thus it illustrates the main molluscan characters: a broad, flat, muscular **foot** for creeping across rocks and holding on to them when disturbed; a **visceral mass** above the foot, containing most of the organs of the body; a **mantle,** or fold of tissue which covers the visceral mass and projects laterally over the edges of the foot; and a hard, calcareous **shell,** secreted by the upper surface of the mantle, as eight separate plates. Like the outer covering of the arthropods, this shell gives protection, but has the disadvantage of making locomotion difficult.

The molluscan digestive system is a single tube, sometimes coiled, consisting of a mouth, pharynx, esophagus, stomach, intestine and anus. The pharynx characteristically contains a rasplike structure, the **radula,**

which, operated by a set of muscles, can drill a hole in another animal's shell, or break off pieces of a plant.* The circulatory system consists of a pumping organ which sends blood through a system of branched vessels and open spaces containing the body organs. Two "kidneys," lying just below the heart, extract metabolic wastes from the blood, and discharge them through pores located near the anus. The nervous system consists of two pairs of nerve cords, one going to the foot, another to the mantle. The ganglia of these are connected around the esophagus, at the anterior end of the body, by a ring of nervous tissue, thus forming the "brain." With the exception of squids and octopuses, the molluscs lack well-developed sense organs.

One usually thinks of snails as having a spirally coiled shell, and many of them do, yet many members of the same class (**Gastropoda**), such

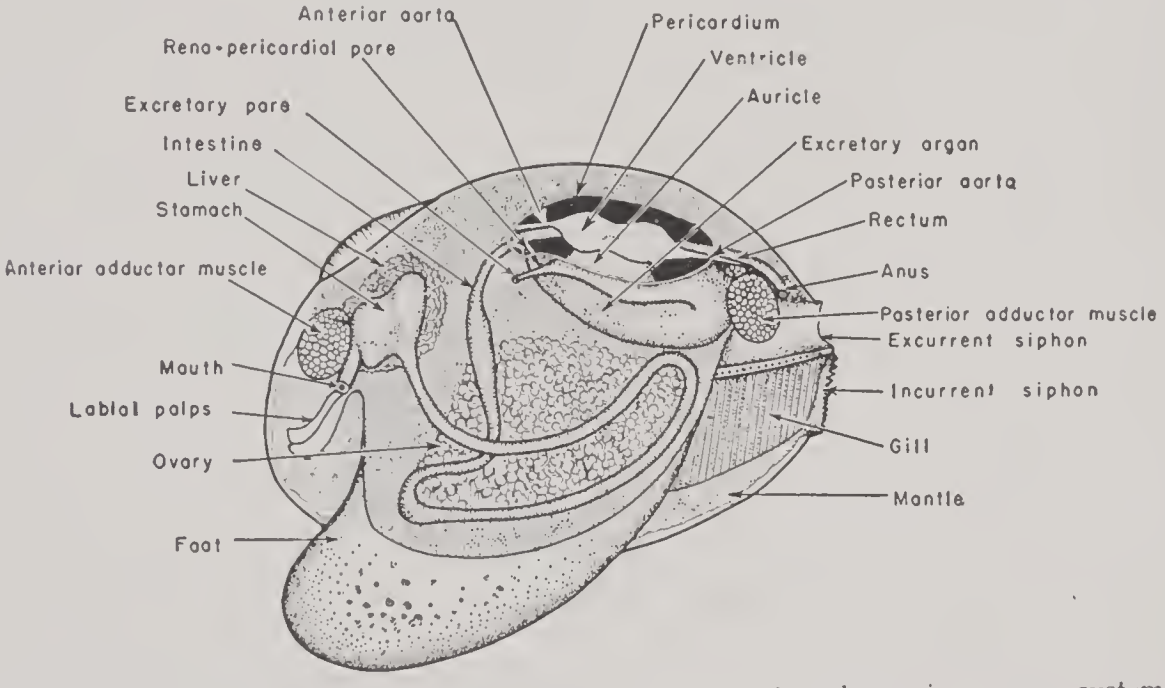


Fig. 59. Longitudinal section of a fresh-water clam, showing the various organ systems. (Hunter and Hunter: College Zoology.)

as the limpets and abalones, have shells like flattened dunce caps, and others, such as the garden slugs and some marine snails, have no shell at all.

Another class of molluses, **Pelecypoda** (meaning hatchet-foot), commonly called bivalves, developed two shells, hinged on the dorsal side and opening ventrally. This arrangement allows the hatchet-shaped foot to protrude for locomotion, and the long, muscular siphon, containing two tubes for the intake and output of water, to be extended. Some bivalves, such as the oysters, are permanently attached to the substrate; others, like clams and mussels, burrow rather slowly through sand or mud by means of the foot. A third type burrows through rock or wood, seeking protected dwellings (the shipworm, *Teredo,* which damages dock pilings and other marine installations, is just looking for a home). Finally, some bivalves, such as the scallops, swim with amazing speed by clapping their two shells together.

* In general, molluscs have this organ, but the bivalves do not have or need such a structure.

Clams (Fig. 59) and oysters obtain food by straining the sea water brought in over their gills by the siphon. The water is kept in motion by the beating of cilia on the surface of the gills, and food particles trapped in the mucus secreted by the gills are carried to the mouth. The innermost, pearly layer of the bivalve shell, made of calcium carbonate (mother-of-pearl), is secreted in thin sheets by the epithelial cells of the mantle. If a bit of foreign matter gets between the shell and the epithelium, the epithelial cells, in order to protect the animal, secrete concentric layers of this substance around the intruding particle; in this way, a pearl is formed.

In contrast to other molluses, squids (Fig. 58) nautiluses and octopuses, comprising the class **Cephalopoda,** are active, predatory animals. By combining the rudimentary head of the chiton type with the molluscan foot they have evolved a specialized, complex head-foot with a large, well-developed "brain" and two big eyes which are strikingly like vertebrate eyes in structure, but develop quite differently as a folding of the skin, rather than as an outgrowth of the brain. This type of independent evolution of similar structures which carry on similar functions in two different, unrelated animals, is known as **convergent** evolution. The foot of the squid and octopus is divided into ten and eight long tentacles, respectively, covered with suckers for seizing and holding the prey. Besides having a radula, the animals have (in the mouth) two strong, horny beaks for killing the prey and tearing it to bits. The mantle is thick, muscular and fitted with a funnel. By filling the mantle cavity with water and ejecting it through this funnel, the animals attain rapid jet propulsion in a direction opposite to that in which the funnel is pointed.

The shell of a nautilus is a flat, coiled structure, consisting of many chambers, built up year by year; each year the animal lives in the latest and largest chamber of the series. The shell of the squid is reduced to a small "pen" in the mantle, and the octopus has no shell at all.

13. The Echinodermata. The echinoderms (spiny-skinned) include the **sea stars, sea urchins, sea cucumbers, serpent stars** and **sea lilies** (Fig. 60)—a group of animals radically different from all other invertebrates. Curiously enough, they appear to be closely related to the vertebrates. The echinoderm larva and those of certain primitive chordates have many features in common. All the 6000 or so species of this phylum are marine, and all have radial, rather than bilateral, symmetry.

A star fish or sea star consists of a central disc from which radiate five to twenty or more arms. On the under side of the disc, in the center, is the mouth. The skin of the entire animal is imbedded with tiny, flat bits of calcium carbonate, some of which give rise to spines. A number of these spines are movable. Around the base of some, especially near the delicate skin gills used in respiration, are still tinier, specialized spines, in the form of pincers; operated by muscles, these keep the surface of the animal free of debris. In order to move, and attack their prey, echinoderms are equipped with a unique hydraulic arrangement called a **water vascular system.** The under surface of each arm is equipped with hundreds of pairs of tube feet—hollow, thin-walled, sucker-tipped cylinders—at the base of which are round muscular sacs.

called **ampullas.** To extend the feet, these sacs contract, forcing water into the feet. The feet are withdrawn by the contraction of muscles in their walls which forces the water back into the ampullas. The cavities of the tube feet are all connected by radial canals in the arms, and these, in turn, are connected by a circular canal in the central disc.

To attack a clam or oyster, the sea star mounts it, assuming a humped position as it straddles the edge opposite the hinge. Then, with its tube

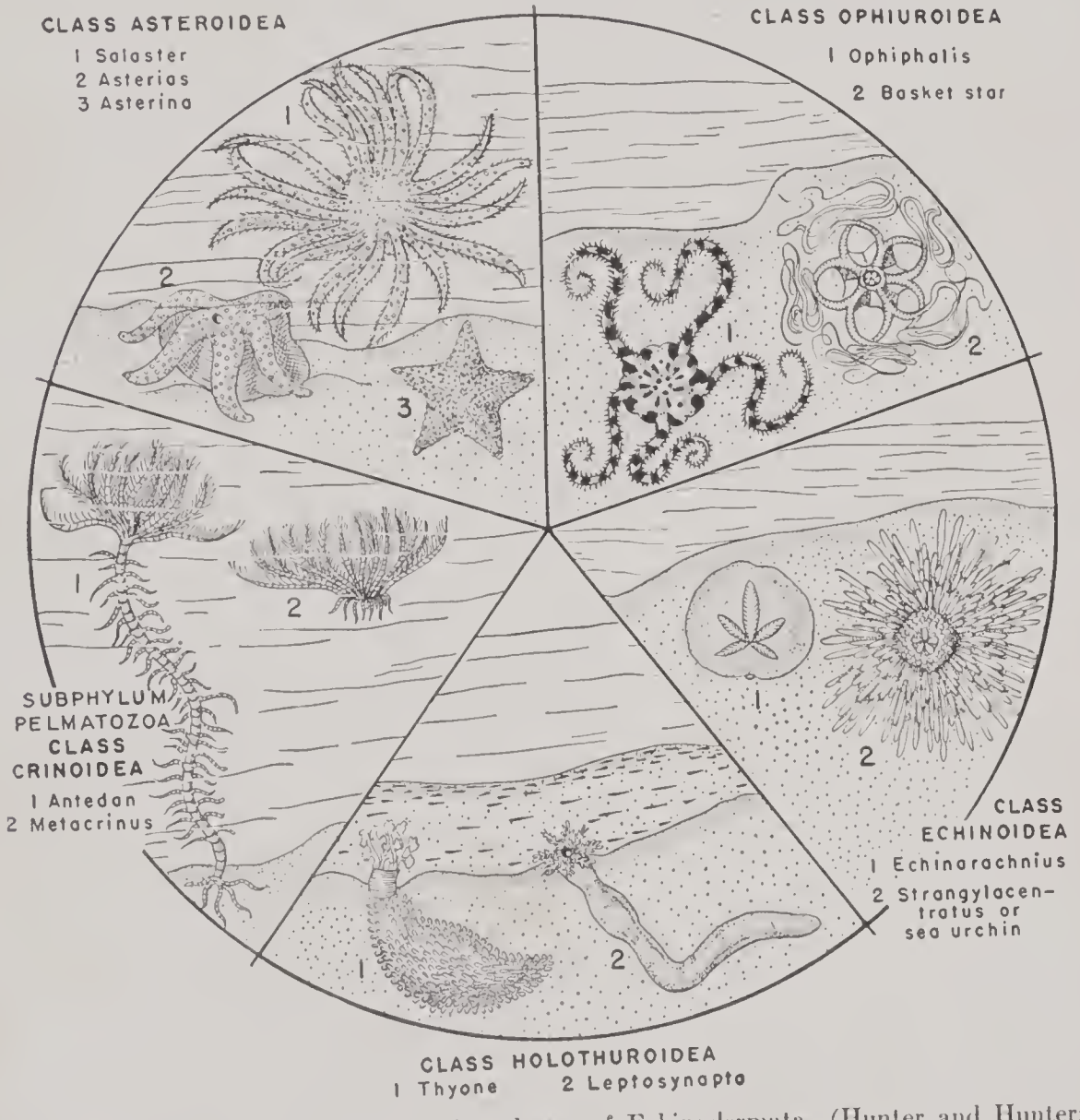


Fig. 60. Some representatives of the five classes of Echinodermata. (Hunter and Hunter: College Zoology.)

feet attached to the two shells, it begins to pull. The clam, of course, reacts by closing its shell tightly. But by using its tube feet in relays, the sea star can outlast the clam, which, becoming exhausted, relaxes, and opens its shell. The sea star then turns its own stomach inside out through the mouth and inserts it into the clam to digest it. The partly digested animal is later taken inside the sea star for further digestion in glands located in each arm. The water vascular system does not enable the star fish to move rapidly, but since it preys upon the slow-moving or stationary clams and oysters, speed of attack is not necessary as it is for most predators.

There are no special respiratory or circulatory systems in these animals; both functions are accomplished by the fluid which fills the large celomic cavity and bathes the internal organs. Nor is there any special excretory system—wastes pass to the outside by diffusion. The nervous system consists of a ring of nervous tissue encircling the mouth, and a nerve cord extending from this into each arm. There is no aggregation of nerve cells which could be called a brain.

A second class of echinoderms, the brittle stars or serpent stars also have a central disc, but their arms are long and slender, enabling them to move rapidly. The arms are discarded and replaced when injured.

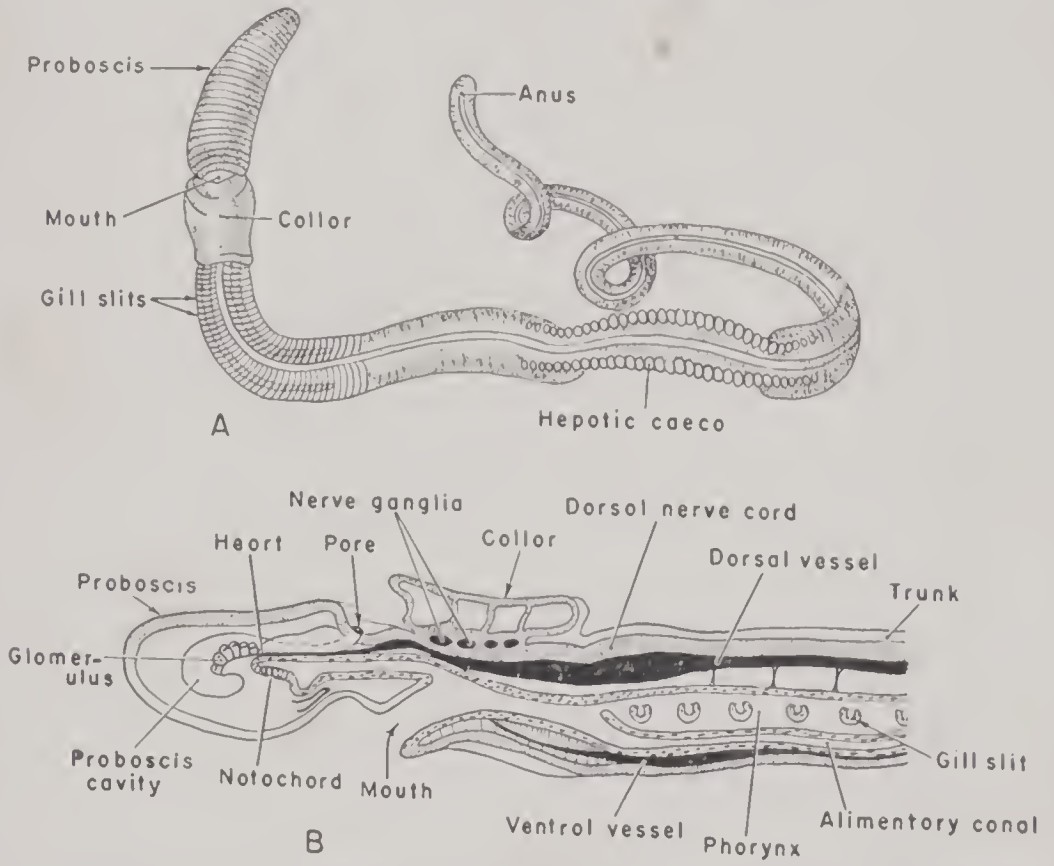


Fig. 61. The acorn worm, *Balanoglossus*, a member of the subphylum Hemichordata. *A*, External appearance; *B*, longitudinal section through the anterior end to show the internal structures. (Hunter and Hunter: College Zoology.)

Sea urchins, a third class of echinoderms, look like animated pincushions, bearing on their rather round bodies long, movable spines between which the tube feet protrude. In these creatures the calcareous plates have fused, forming a spherical shell, and in the center of the under surface of this is the mouth. The tube feet, arranged in five bands on the surface of the shell, are longer and more slender than those of sea stars, but the water vascular system is otherwise similar.

Sea cucumbers, another class of the spiny-skinned phylum, are obviously named, for many of them are green and about the size and shape of a gherkin. Like the members of several other phyla, these animals have a circle of tentacles around the mouth, and, in common with the starfish, they have a water vascular system, but they may or may not have external tube feet. When menaced, they eject most of their internal organs through the mouth, and the squirming mass apparently diverts the attention of the predator. Meanwhile, the sea

cucumber escapes, eventually to grow a new set of internal organs. The bodies of sea cucumbers are quite flexible, hollow muscular sacs.

The crinoids, or sea lilies, are rather like a starfish turned mouth side up, with a number of arms extending upward and a stalk which attaches the animal to the sea bottom. There are many more fossil than living species.

The foregoing description does not exhaust the great variety of animals. In addition to these phyla, there are other groups of invertebrates sometimes put in phyla of their own, sometimes classified under other phyla which are not important enough to be discussed here.

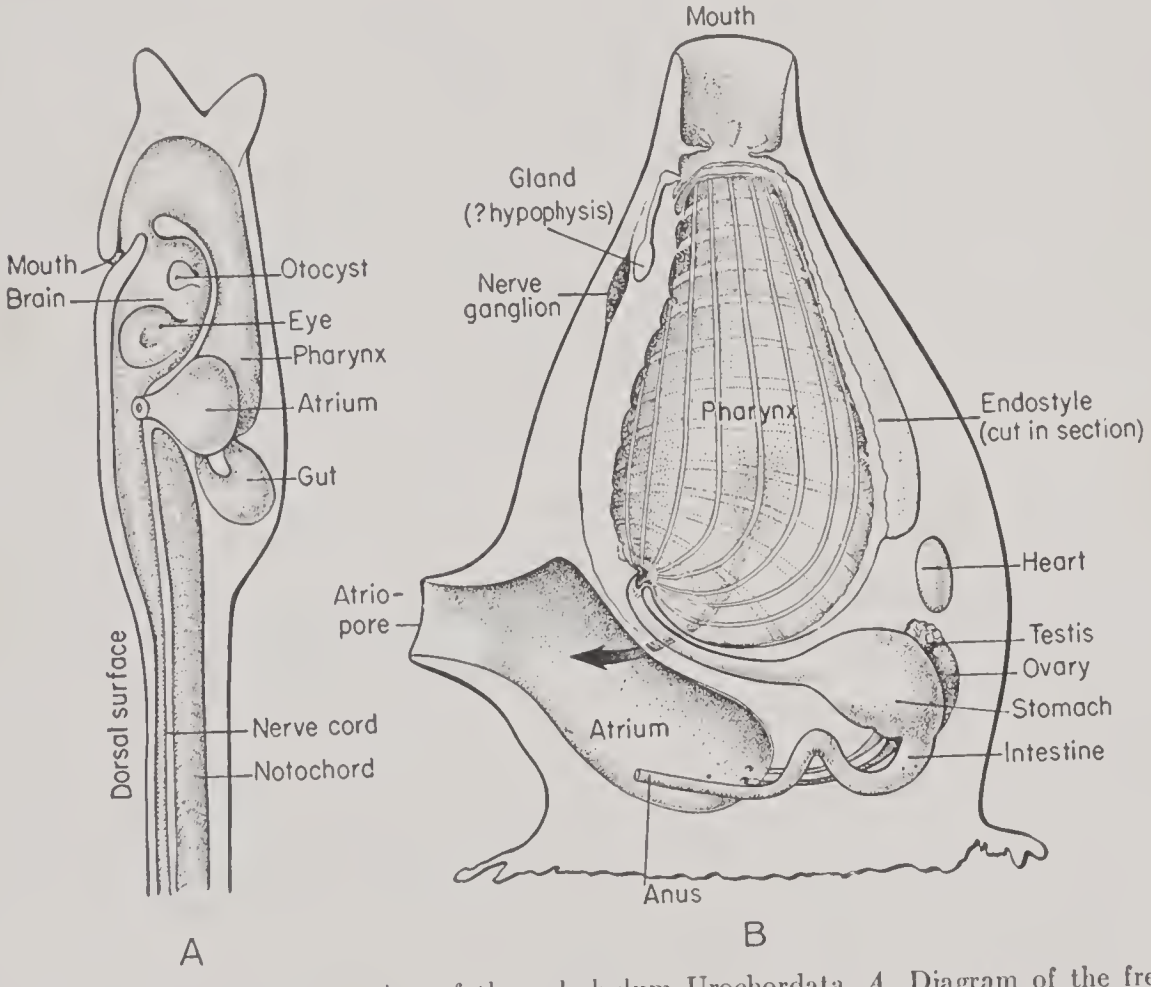


Fig. 62. A tunicate, a member of the subphylum Urochordata. *A*, Diagram of the free-swimming larva, anterior end up (the otocyst is an organ of equilibrium). *B*, Diagram of the sessile adult which develops from the anterior part of the larva. (After Delage and Herouard; Romer, A. S.: The Veterbrate Body.)

14. The Chordata. The last great phylum of animals, that to which man belongs, is the phylum Chordata, whose members are distinctive in having a notochord, a dorsal, hollow nerve cord, and gill slits.* In addition to the main classes—the fishes, amphibia, reptiles, birds and mammals, which make up the subphylum, **Vertebrata,** characterized by a cartilaginous or bony vertebral column—the phylum Chordata includes three subphyla of lowly creatures which show the chordate characteristics to some extent, and are extremely interesting examples of possible connecting links between the vertebrates and invertebrates.

* The latter are not always visible in the adult form.

The title of "chordate-least-like-the-vertebrates" falls to the **acorn worm,** a burrowing marine animal (Fig. 61). On its anterior end is a muscular proboscis used in travelling through the sand; behind this, a collar; and then a long, soft, wormlike body. The mouth is on the lower side of the body at the base of the collar, and just behind the collar, perforated by many gill slits, is the pharynx, through which water passes. As it burrows along, the animal feeds on organic matter in the sand. The nervous system is a diffuse network over most of the body, but concentrated into dorsal and ventral nerve cords in the anterior region. Only the dorsal nerve cord extends into the collar, where it becomes thick and hollow. There is a short, rodlike outgrowth from the anterior end of the digestive tract which extends into the cavity of the proboscis. Although this is called a "notochord," it is not clear whether it really corresponds to the notochord of other chordates. The

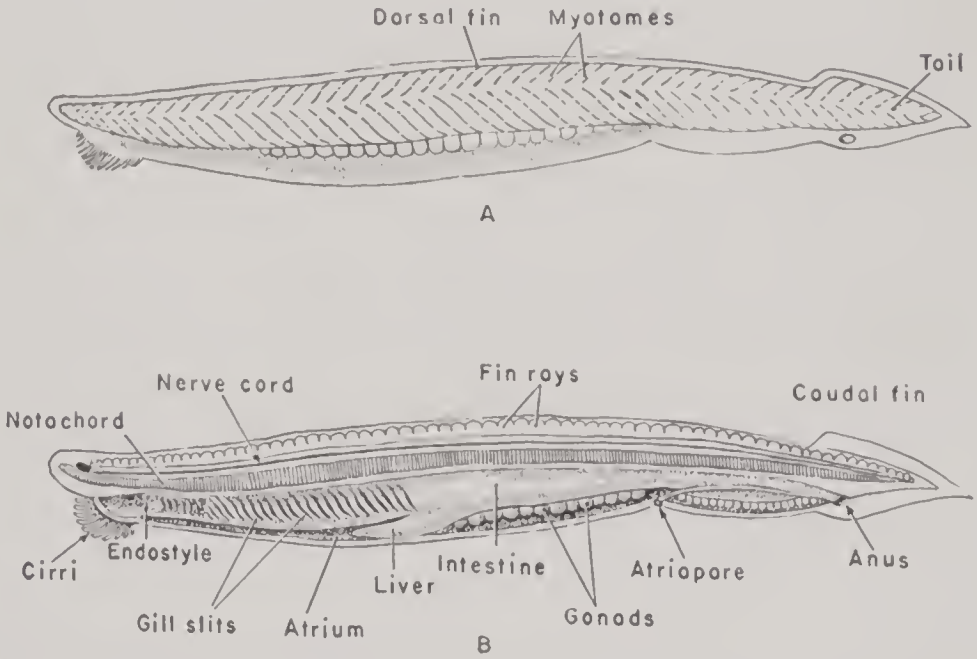


Fig. 63. External view and a longitudinal section of amphioxus, a member of the subphylum Cephalochordata. (Hunter and Hunter: College Zoology.)

acorn worm has, then, to a limited degree, the three chordate characteristics. Its larva, however, is much like that of the echinoderms and is often mistaken for it, but of course the later development of the two forms is quite different.

A second subphylum is composed of the **sea squirts** or **Tunicates** (Fig. 62), most of them attached forms unlike the other chordates; indeed, the primitive members are often mistaken for sponges or coelenterates. The larval form of the tunicates, however, is typically chordate, superficially like a tadpole. It has a pharynx with gill slits, and a long tail containing a notochord and dorsal nerve cord. The larva eventually becomes attached to the sea bottom, and loses its tail, notochord, and most of its nervous system. In the adult, therefore, only the gill slits suggest that it is a chordate.

In the organisms of the third chordate subphylum, the **Cephalochordata,** all three chordate characteristics are highly developed. There is a

notochord extending from the tip of the head to the tip of the tail, a large pharyngeal region, with many pairs of gill slits, and a hollow, dorsal nerve cord (Fig. 63). The cephalochordates are small, translucent, fishlike animals, a few inches long, which live in shallow seas all over the world, either swimming freely or burrowing in the sand near the low tide line. They feed by drawing a current of water into the mouth (by

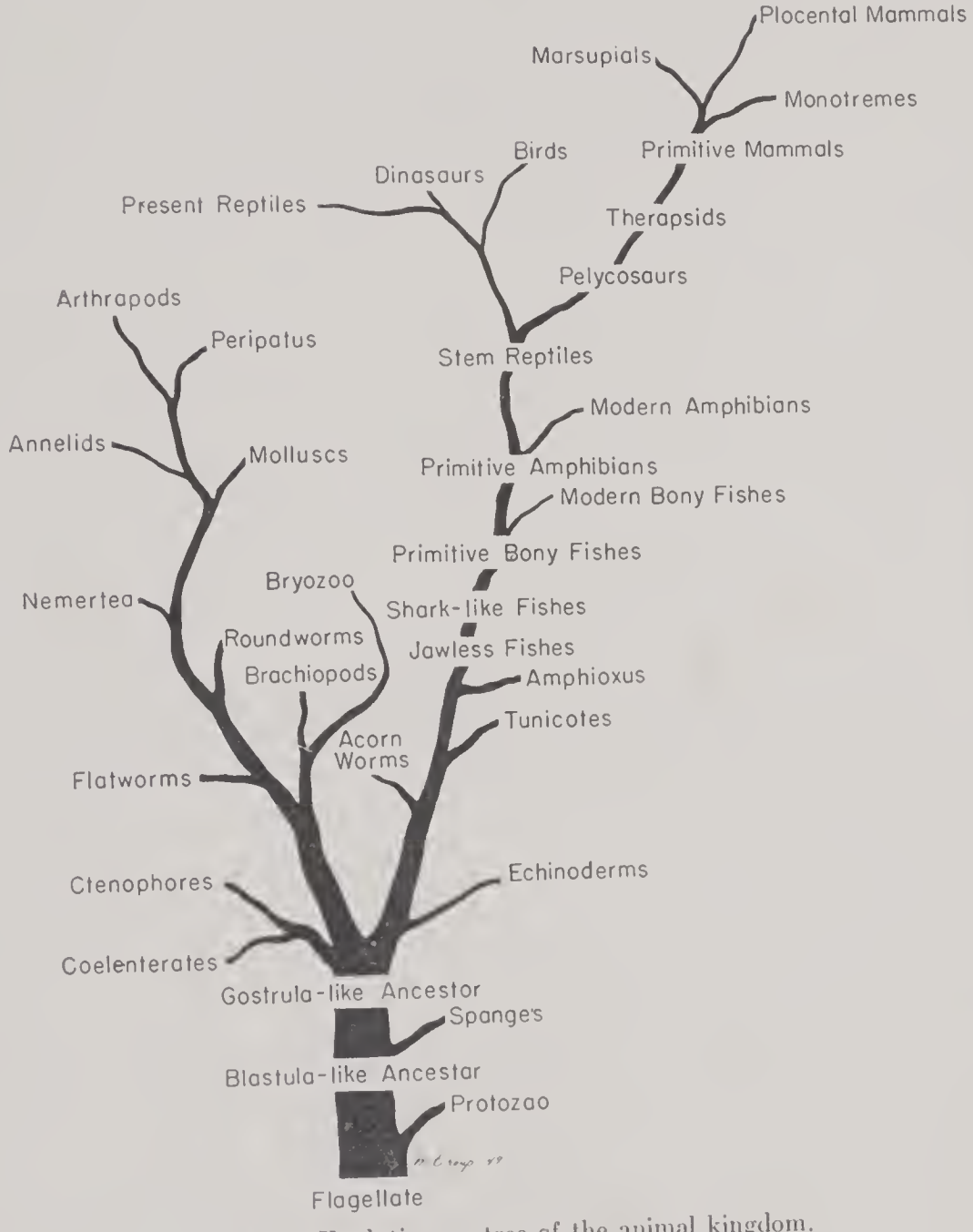


Fig. 64. Evolutionary tree of the animal kingdom.

the beating of cilia) and straining out the microscopic plants and animals. Although superficially similar to fishes, they are much more primitive, for they lack paired fins, jaws, sense organs and a brain. It is generally believed that the cephalochordate amphioxus is rather similar to the primitive ancestor from which the vertebrates evolved. In contrast to the invertebrates, the blood of this animal flows anteriorly in the ventral vessel and posteriorly in the dorsal vessel.

The **Vertebrates** are distinguished by an internal skeleton of cartilage or bone, the anterior end of which, called the brain case, encloses the enlarged, anterior end of the nerve cord. Additional characteristics are paired eyes, which developed as outgrowths of the brain, and paired ears, originally organs of equilibrium. The vertebrates also have a ventral, muscular heart which pumps blood around a closed circulatory system.

The classes of the subphylum Vertebrata are as follows: the **Agnatha**, the jawless fishes, such as the lamprey eels; the **Placodermii**, earliest of the jawed fishes, known only from fossils; the **Chondrichthyes**, the sharks and rays with cartilaginous skeletons; the **Osteichthyes**, the bony fishes; the **Amphibia**, the frogs and salamanders; the **Reptilia**, the snakes, turtles and alligators, plus a host of fossil forms like the dinosaurs; the **Aves**, the birds; and the **Mammalia**, the warm-blooded, fur-bearing animals that suckle their young.

The various members of the animal kingdom cannot be placed on a single scale ranging from lowest to highest, for evolution has occurred in the manner of a branching tree, rather than in a continuous series (Fig. 64). We cannot say, for example, that the starfish is "higher" or "lower" than the oyster; the two forms are simply representative of the main trunks of the evolutionary tree—one giving rise to echinoderms and chordates, the other to flatworms, nemerteans, annelids, arthropods and molluscs. Between the two groups are deep-lying differences of structure and development which will be discussed in Chapter 27.

QUESTIONS

1. Distinguish between homologous and analogous structures. Why must classifications be based on the former?
2. What is meant by the protoplasmic level of the animal kingdom?
3. What are the outstanding characteristics of protozoa?
4. How do sponges obtain food and water?
5. Why are coelenterates said to represent the tissue level of the animal kingdom?
6. What are "flame" cells, and how do they operate?
7. Distinguish between the organ level and the organ system level of organization.
8. What is the fundamental difference between a tape worm, an earthworm and a round worm such as ascaris?
9. Describe the peripatus. What is its significance from the evolutionary standpoint? If you were classifying it, would you place it with the annelids, the arthropods, or by itself?
10. Explain the similarities between a tick and a lobster.
11. What is convergent evolution? Does it result in homologous organs?
12. What is the evidence for believing the echinoderms to be more closely related to the vertebrates than to the other invertebrates?
13. What are the three main characteristics of the phylum Chordata?
14. Give the phylum, subphylum and class to which man belongs, and name three other animals which each division includes.
15. An animal is multicellular, has no digestive system, and its body is perforated with pores: what is it?

SUPPLEMENTARY READINGS

Buchsbaum, R.: *Animals without Backbones*. 2d ed. Chicago, University of Chicago Press, 1948.

A popular book on invertebrates, with excellent illustrations.

Coker, R. E.: *This Great and Wide Sea*. Chapel Hill, University of North Carolina Press, 1947.

A popular discussion of oceanography and deep-sea animals.

Comstock, J. H., and Gertsch, W. J.: *The Spider Book.* 2d ed. New York, Doubleday, Doran & Company, Inc., 1940.
An interesting, semipopular account of spiders.

Hegner, R. W.: *Parade of the Animal Kingdom.* New York, The Macmillan Company, 1937.
A popularly written book with many illustrations of animals.

Hunter, G. W., and Hunter, F. R.: *College Zoology.* Philadelphia, W. B. Saunders Company, 1949.
A well-written and illustrated discussion of both vertebrates and invertebrates.

Ricketts, E. F., and Calvin, F.: *Between Pacific Tides.* Stanford, Stanford University Press, 1939.
An interesting description of the seashore animals found on both rocky and sandy beaches; well illustrated.

Scheer, B. T.: *Comparative Physiology.* New York, John Wiley & Sons, Inc., 1948.
Many interesting facts about the methods used by different animals to carry on their basic life functions.

Wheeler, W. M.: *The Social Insects, Their Origin and Evolution.* New York, Harcourt, Brace and Company, Inc., 1928.
A fascinating account of termites and ants.

Wilson, D. P.: *They Live in the Sea.* London, Collins, 1947.
A popular description of some seashore animals, with many fine photographs.

PART III

THE ORGANIZATION OF THE BODY

CHAPTER 8

THE BLOOD

BLOOD is a tissue just as muscle, bone and epithelia are tissues, being composed of a group of cells with specific functions. It is a particularly convenient tissue to study because it can be easily obtained: a sample taken from a small skin puncture is not injured in any way, and the cells may be observed in their normal condition. For this reason, much of the work on the relationship of cells to their environment has been done with blood.

The amount of blood in a person depends upon his weight; an average man weighing 150 pounds has approximately 5 quarts of blood, just the quantity of oil in the crankcase of most cars. Blood performs a number of important functions: it carries food and oxygen to all cells, and removes the waste products of metabolism; it transports the secretions of the endocrine glands, the hormones; it has the ability to equalize the water content of the body, giving off or taking up water from the other tissues as needed; and it is an important factor in equalizing body temperature, cooling such organs as the muscles where excessive heat is produced, and heating others (such as the skin) where the loss of heat is greatest. Finally, through the action of the white blood cells, it plays a vital role in the body's defense against disease organisms.

As it flows from a wound, blood appears to be a sticky, homogeneous, crimson fluid, a little heavier than water. Chemical analysis shows it to be just on the alkaline side of neutrality, with a *p*H of about 7.39. Microscopically, it is composed of a slightly yellowish liquid, the **plasma** (constituting about 55 per cent of whole blood), in which float particles, the **formed elements** (comprising the remaining 45 per cent). There are variations in these proportions even in healthy people; after profuse perspiration the plasma may constitute only 50 per cent of the whole blood, and after drinking a great deal of water or beer it may be increased to 60 per cent.

There are three types of formed elements: **red blood cells**, which give blood its color, colorless **white blood cells**, and **blood platelets**, consisting of tiny fragments broken off from large cells in the bone marrow, which are important in initiating blood clotting. The formed elements are heavier (specific gravity, 1.09) than plasma (specific gravity, 1.03), and may be separated from it by centrifuging, but as it flows through the body the blood is constantly agitated, thus preventing this separation from occurring.

I. PLASMA

Plasma is an extremely complex and rather variable solution containing proteins, amino acids, carbohydrates, fats, salts, secretions of the endocrine glands, enzymes, antibodies and dissolved gases. It has

not been completely analyzed, and some of its constituents are still unknown. About 90 per cent of plasma is water, about 7 per cent is protein, about 0.9 per cent is salts, and 0.1 per cent is glucose; the other substances are present in minute amounts. In spite of the fact that plasma is constantly losing and taking up materials, it maintains the relatively constant composition necessary for life. This is made possible by a complex set of relationships between the organs of the body. Any change in the composition of the blood initiates a readjustment of some kind to restore the normal equilibrium.

The proteins in plasma necessary to maintain the water balance of the blood include fibrinogen (important in blood clotting), serum albumin and serum globulin—all of them colloidal sols. The proteins are responsible for the viscosity of blood, which is about six times that of distilled water. Any deviation from the normal impairs circulation. Since the plasma protein molecules are too large to pass through the walls of blood vessels, they exert an osmotic pressure, causing water to pass from the surrounding tissues into the blood. Water tends to filter back out of the capillaries because of the filtration pressure, and the osmotic pressure of the plasma proteins keeps the amount of water constant. Under certain conditions, such as shock, the balance is upset, because the blood vessels become permeable to the plasma proteins, and water passes out of the blood vessels. In some diseases the kidneys permit plasma proteins to pass through into the urine, thereby lowering the concentration of proteins in the blood. The osmotic pressure no longer balances the filtration pressure, so that water passes from the blood into the body tissues, resulting in the condition known as **edema**. The plasma proteins are also important for recovery after a hemorrhage. Loss of blood causes a decrease in the blood pressure all over the body, and a corresponding decrease in the filtration pressure. Since the percentage of proteins in the remaining plasma is unchanged, the osmotic pressure becomes greater than the filtration pressure. Therefore, water passes from the tissues into the blood vessels and the lost blood is partly replaced by this liquid. This balance between osmotic and filtration pressure is just one of the many automatic devices of the body which maintain the *status quo*.

Plasma contains a variety of salts—compounds of sodium, potassium, calcium and magnesium with chloride, carbonate, phosphate and sulfate ions. The total concentration of all these salts is about 0.9 per cent in mammals, and slightly less in the lower animals. A marked change in the concentration of any of the salts results in profound changes in cellular activity.

The concentration of glucose in plasma varies from about 0.08 to 0.14 per cent, averaging 0.1 per cent. The glucose in the blood is transported from the intestines (where it is absorbed into the body) and from storage centers in the liver to all body cells, where it is removed and oxidized to release energy. If the concentration of glucose falls to 0.04 per cent or less, the irritability of certain brain cells is greatly increased, with the result that very slight stimuli cause them to send impulses to muscles and bring about muscular twitching, convulsions and, eventually, death.

When whole blood or plasma is removed from the blood vessels, it **clots,** or changes into a gelatinous mass. If this is allowed to stand for a time, it shrinks and squeezes out a light, yellow liquid called **serum.** Plasma, then, is the liquid part of whole blood; serum is the liquid left after clotting has occurred. The chemical composition of serum is almost identical with that of plasma, the chief difference being the absence from serum of fibrinogen, one of the plasma proteins. In the clotting process the fibrinogen changes from a sol to a gel and forms the firm part of the clot.

1. Plant Sap. The material in the higher plants which is somewhat analogous to blood plasma is the plant sap. This is a complex solution of many substances, both organic and inorganic, which is transported from one part of the plant to another. The substances present and their concentrations vary greatly in different plants and in various parts of the same plant. Water is absorbed by the epidermal cells of the roots and moved to all parts of the plant. Sugar is manufactured in the leaves and carried to other cells to be used for the release of energy or for the production of more complex carbohydrates, fats and proteins. Stored food in the root or stem is transported to other parts of the plant to be utilized.

The simpler, lower plants have no specialized vascular tissues: all the cells are involved in the movement of materials. In the higher plants, where substances must be carried long distances, special vascular tissues —xylem and phloem—have evolved to perform the task. A few plants have an additional latex system, containing the milky substance **latex,** which is probably an additional vascular tissue. Latex is rich in food substances (carbohydrates and proteins), and certain plants containing it yield commercially valuable products such as rubber, chicle and opium.

Plant saps are much more variable in their composition than is blood plasma. As much as 98 per cent of sap may be water. Salts of sodium, potassium, calcium and magnesium are most abundant, as in plasma, and traces of others are also present. Saps contain varying quantities of glucose and other sugars, depending on the species, time of year, part of the plant and other factors. They also contain waste products of metabolism, proteins, enzymes, hormones, dissolved oxygen and carbon dioxide, and organic acids such as the citric acid in lemons and the malic acid in apples. Plant saps differ from plasma in that they are usually acid rather than alkaline; most of them have a *p*H between 4.6 and 7.0. The most acid plant known is the begonia, with a *p*H of 0.9.

II. FORMED ELEMENTS OF THE BLOOD

2. Red Corpuscles. The red blood cells, or **erythrocytes,** are biconcave discs between 7 and 8 microns in diameter (Fig. 65). Unlike most cells, they have no nucleus. Supporting them is an internal elastic framework which maintains the disc shape, but permits the cell to bend and twist and thus pass through a blood vessel smaller than its diameter. Erythrocytes are not capable of active movement themselves—they merely float in the blood stream and are moved about by the beating of the heart. There are, on the average, about 5,400,000 red blood cells per

cubic millimeter of blood in the adult male, and about 5,000,000 in the adult female. Newborn infants have a larger number, between 6,000,000 and 7,000,000 per cubic millimeter. This number gradually decreases throughout childhood to the adult number.

There are about thirty trillion red blood cells in the human body. This figure is estimated from a small sample, by a procedure known as the **red cell count.** Since the number of red cells per cubic millimeter is an important factor in determining a person's general health, almost all clinical examinations include such an analysis. The device for counting red blood cells, called a **hemocytometer,** includes a diluting pipette and a counting chamber. Blood drawn from the patient is first accurately diluted 200 times, by using the diluting pipette to draw blood up to the 0.5 mark and then adding the proper diluting fluid to bring the combined blood and fluid to the 101 mark. The blood and diluting

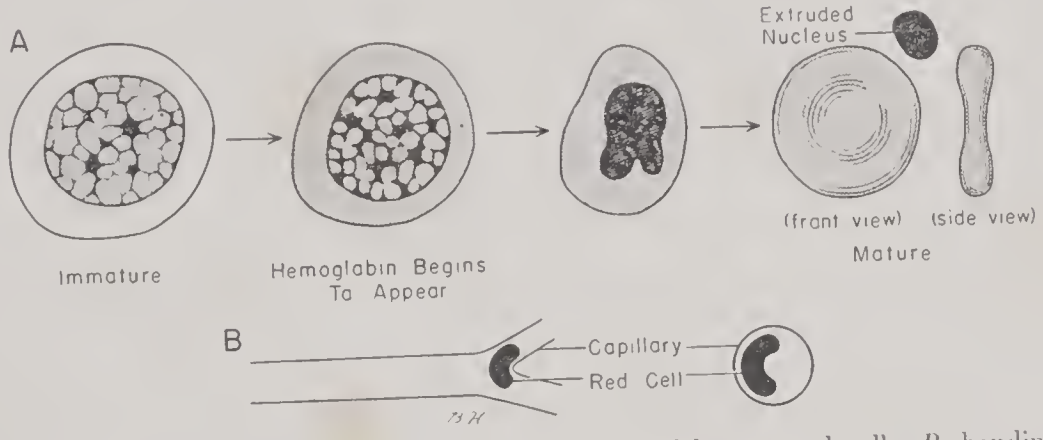


Fig. 65. Red blood cells. *A*, Stages in the formation of human red cells; *B*, bending and twisting of red cells as they pass through capillaries. Their supporting elastic framework causes them to resume their normal disc shape after the tension is released.

solution are then carefully mixed in the pipette, and the diluted blood is placed on the stage of the counting chamber. This stage has two sets of fine lines 50 microns apart, ruled at right angles to each other, thereby making squares 50 microns on a side. On each side of the counting chamber is a ridge of glass exactly 100 microns higher than the surface of the chamber. When a flat glass cover slip is placed on the two ridges covering the counting chamber, small cubes 50 by 50 by 100 microns are delineated—each one a volume $\frac{1}{4000}$ of a cubic millimeter. When the diluted blood is placed on the stage, the number of red cells in a number of these small cubes is determined, an average taken, and a simple calculation made to convert the number of red cells in $\frac{1}{4000}$ cubic millimeters of diluted blood to the number of red cells in 1 cu. mm. of undiluted blood.

3. Hemoglobin and the Transport of Oxygen. The red cells contain the important red pigment **hemoglobin,** a protein with four atoms of iron per molecule. In a normal person each 100 gm. of blood contains 15 to 16 gm. of hemoglobin. This protein has the ability to form a loose chemical union with oxygen when that element is present in abundance. When the red cells reach a part of the body where oxygen is scarce, oxyhemoglobin (the oxygen-hemoglobin compound) releases the oxy-

gen and makes it available to the tissues. Through this property of hemoglobin, the red cells carry out their chief function, the transportation of oxygen from the lungs (gills in fish) to all the tissues of the body. They also assist in the return of carbon dioxide to the lungs.

Carbon monoxide, present in commercial illuminating gas and in the exhaust gas of automobiles, also forms a compound with hemoglobin. This gas is poisonous because the carbon monoxide hemoglobin, being unable to combine with oxygen, cannot transport it to the cells. If the air breathed contains only half of 1 per cent of carbon monoxide, about half the blood hemoglobin is in the form combined with carbon monoxide, and only half is left to transport oxygen. This has the same effect as the sudden loss of half of one's red cells. The union of hemoglobin with carbon monoxide is reversible, just as is the union with oxygen, but the decomposition of carbon monoxide hemoglobin is slow, and several hours in an atmosphere free of carbon monoxide are required to free the blood of it. People suffering from carbon monoxide poisoning should therefore be given fresh air, and artificial respiration if necessary.

In some types of disease, such as blackwater fever, a complication of malaria, the red blood cells are destroyed and hemoglobin is released to the plasma and excreted in the urine, making it black. Many diseases cause a decrease in the amount of hemoglobin in the blood, a condition known as **anemia.**

4. Life History of Red Cells. Red blood cells are constantly being destroyed and new ones manufactured, yet the total number remains remarkably constant. These cells are produced in the **red bone marrow,*** which lies in the hollow cavities of most of the bones, and consists of a network of connective tissue cells. The red cells are actually formed by the rapid division of cells which line the blood vessels of the red marrow. Normal cell division is possible only in cells with a nucleus, and the precursors of the red blood cells in the red bone marrow are unspecialized cells with a nucleus and no hemoglobin (Fig. 65). After undergoing its last division, each cell is gradually transformed into a mature corpuscle by a process which includes the loss of the nucleus, the manufacture of hemoglobin, and the change to the biconcave disc shape. During the formation of red cells the blood vessels of the red bone marrow are closed, preventing the passage of blood. As soon as the cells are completely formed, the vessels open and the new cells are swept out into circulation. There are many thousands of these blood vessels in the red marrow; at any one time some are open and others are closed, engaged in red cell production. In certain abnormal conditions, red cells are manufactured too rapidly, and immature cells still containing a nucleus are released to the blood stream.

Recent estimates, obtained from tracer experiments, indicate that red cells circulate, on the average, about 127 days before cells in the liver and spleen destroy them. The spleen, an oval organ about 5 inches long lying to the left of the stomach, is connected only to the blood stream, and serves as a reservoir for red cells. The walls of the blood vessels of the spleen and liver are lined at intervals by cells which have the ability

* *Yellow marrow* is made of cells modified for the storage of fat.

to engulf or **phagocytize** red blood cells and thus destroy them. Why they should destroy some red cells and not others is unknown; presumably, only the old, worn-out cells are demolished.

In the liver, hemoglobin is broken down chemically into a number of simpler substances. At least some of the iron is carried back to the red bone marrow and re-used in the formation of new hemoglobin. Another of these substances is converted into **bile pigments,** excreted by the liver down the bile duct into the intestine, from which they finally pass from the body in the feces. These pigments are largely responsible for the color of the feces; if the bile duct is blocked by a gallstone, the pigments are prevented from entering the intestine and the feces are almost colorless.

Estimates indicate that in an average adult, between ten and fifteen million red cells are destroyed and formed per second, every day throughout life.

The constancy of the number of red cells provides us with an excellent example of **dynamic equilibrium.** New cells are constantly formed and old cells are constantly destroyed, yet because of a balance between the formative and destructive processes, the total number of red cells remains relatively constant. A clue to the mechanism involved in maintaining this equilibrium lies in the fact that a sojourn of a few weeks at a high altitude increases the red count to six or seven million per cubic millimeter. Experiments show that this is due simply to the decreased amount of oxygen present in the air. The increase in red cells can be produced at sea level in experimental animals kept in a pressure chamber where the atmosphere has a lowered oxygen content similar to that of air at high altitudes, but a total pressure similar to that at sea level. A reduced amount of oxygen in the air is reflected in the reduced amount of oxygen in the blood, and the cells in the red bone marrow respond to this decreased oxygen content by producing more red cells. Why and how they are able to respond precisely in this way is unknown.

The cells in the spleen and liver ordinarily prevent an excess of red cells by increasing the rate of red cell destruction. These two basic processes, plus other secondary factors, keep the number of red cells constant. If the number drops for any reason—hemorrhage, increased red cell destruction, or disease—the amount of oxygen is correspondingly reduced, since the oxygen in blood is almost exclusively in the red blood cells. Oxygen lack stimulates the red bone marrow to increase its rate of cell formation in order to make up the deficit. As the number of red cells returns to normal, the stimulus (oxygen deficit) is removed, and the red bone marrow returns to its regular rate of manufacture.

5. Oxygen-Carrying Devices in Other Organisms. All other mammals have red cells similar to those of man—non-nucleated, biconcave discs containing hemoglobin. The other vertebrates, including birds, reptiles, amphibians and fishes, have oval-shaped red cells containing hemoglobin, but with nuclei. The red cells of some of the lower forms are much larger than those of man—a frog's red corpuscles are about 35 microns on the long axis.

There is a variety of oxygen-carrying devices among the invertebrates.

A few worms have blood cells containing hemoglobin, but in others, such as the earthworm, the blood pigment is dissolved in the plasma, instead of in cells. The blood of other invertebrates is characterized by different blood pigments: that of crabs, for instance, is blue-green, owing to **hemocyanin,** a blood pigment containing copper instead of iron.

Plants have neither blood cells nor blood pigments and no need for them, since most of the cells are exposed to the air or to oxygen in the soil. Other cells, unable to obtain oxygen directly, get it by means of air spaces and canals which penetrate to all parts of the plant.

Hemoglobin and other blood pigments are related to substances known as **respiratory enzymes,** common to all cells and involved as catalysts in the utilization of oxygen and the release of energy by the chemical breakdown of food. Their interactions are complex and not completely understood. Some of them, the **cytochromes,** contain iron, while others contain copper. These catalysts enable the cell to carry on

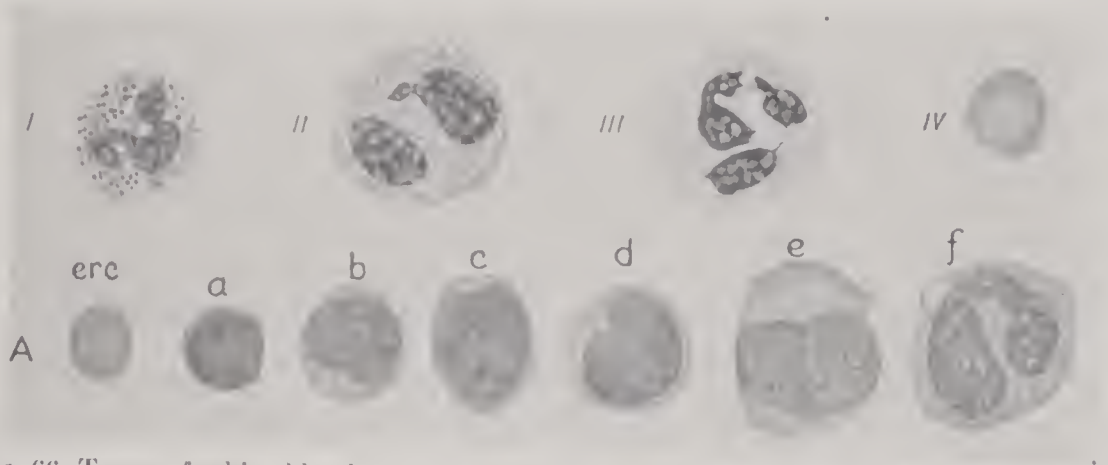


Fig. 66. Types of white blood cells. *I*, Basophil; *II*, eosinophil; *III*, neutrophil; *a–d*, lymphocytes; *e–f*, monocytes; *IV* and *erc*, red blood cells drawn to the same scale. (Maximow and Bloom.)

oxidations rapidly at relatively low temperatures—processes which can be duplicated in the test tube only at temperatures incompatible with life, and at much lower speeds.

6. White Corpuscles. White blood cells, or **leukocytes,** differ considerably from red cells: they contain no hemoglobin and hence are colorless; they retain the nucleus when mature and circulating in the blood stream; and there are five kinds of them. Moreover, white cells have the ability to move about freely, in a manner similar to that of the single-celled ameba and hence called ameboid motion. Unlike the passive red cells, then, they can move against the current and even slip through the walls of blood vessels, whence they migrate to almost every tissue of the body.

White blood cells are much less numerous than red ones; on the average, there are about 7000 white cells per cubic millimeter. Considerable fluctuations in this number (from 5000 to 9000 per cubic millimeter) occur in different people, and even in the same person at different times of the day. The white count is lowest in the early morning and highest in the afternoon. To some extent the white cell count is an index of nourishment; poorly nourished people have lower than normal white counts and consequently lower resistance to disease and infection. A

reduction to 500 or less per cubic millimeter is fatal. In counting the number of white cells, the same principle is used as in counting red cells; the blood is diluted less (only ten times instead of 200), and the diluting fluid contains a substance (acetic acid) to destroy the red cells which otherwise would interfere with the count. The solution is stained with gentian violet to make the white cells easily visible. The diluted blood is placed in a counting chamber, the white cells in a known volume are counted, and proper corrections result in a figure representative of the number of white cells per cubic millimeter of undiluted blood.

The five types of white cells (Fig. 66) can be differentiated by staining the blood with Wright's stain or some other dye.

The **lymphocytes,** the smallest of the white cells, are between 8 and 9 microns in diameter. They have a large nucleus, either spherical or slightly indented, which is colored a dark blue-purple by Wright's stain. Their cytoplasm is scant, forming a thin layer around the nucleus. It is free from granules and stains a light, robin's-egg blue. Lymphocytes are less motile than the other white cells.

The largest of the white cells, the **monocytes,** vary from 12 to 20 microns in diameter. Their nucleus is indented considerably, varying from a bean to a horseshoe shape, and stains a muddy purple. The cytoplasm is abundant, nongranular, and stains slate-blue. The monocytes are motile and have the power to engulf bacteria.

The next three types, **neutrophils, eosinophils** and **basophils,** are similar in many ways. All have nuclei divided into from two to five lobes which are connected by a thread of nucleoplasm; all have granules of some sort in the cytoplasm; and all are between 9 and 12 microns in diameter. The nuclei stain a uniformly dark purple, but the cytoplasmic granules stain differently. All three types are motile and capable of engulfing bacteria, but in the neutrophils these capacities are greater than in the others. Their nuclei contain from three to five lobes, and their small cytoplasmic granules stain a pale lavender. The eosinophils have two-lobed or three-lobed nuclei and large cytoplasmic granules which stain bright red. The basophils usually have a two-lobed nucleus and large, deep blue-staining cytoplasmic granules.

The proportion of white cells belonging to each class is determined by the **differential white cell count.** This consists in smearing a drop of blood thinly and evenly on a glass slide and staining it with Wright's stain. The smear is then examined under the microscope, and several hundred white cells are counted and classified. In a normal person, 60 to 70 per cent of the white cells are neutrophils, about 25 per cent are lymphocytes, 5 to 10 per cent are monocytes, 1 to 4 per cent are eosinophils, and about 0.5 per cent are basophils.

Some biologists credit white cells with the ability to aid the absorption of fat from the intestine into the lymph system. Their chief function, however, is to provide the body with protection against disease organisms. When the body is invaded by bacteria or other disease-causing agents, the white cells engulf and destroy the intruders by the process of phagocytosis. This is accomplished by means of projections which surround the germs while the cells digest them.

When bacteria enter the body—through a wound, for example—they begin to destroy the cells in that region by giving off poisonous chemicals or by attacking them directly. The local blood vessels respond by dilating and bringing in an extra amount of blood. This increase causes a characteristic reddening and higher temperature in the region, known as **inflammation.** When fluid enters the tissue from the blood stream, swelling results. The white cells, especially the neutrophils, migrate through the walls of the blood vessels and phagocytize the invaders and the remains of any destroyed cells from that region. In the process some of the white cells are killed. The aggregation of dead tissue cells, bacteria, and living and dead white cells forms a rather thick, yellowish fluid called **pus.** The white cells apparently are guided to points of infection by chemicals given off by the invading organisms.

After the bacteria have been successfully destroyed, the lost tissue must be replaced. Some of the tissues of the body have the ability to regenerate by the multiplication of neighboring cells; others have only a limited ability to regenerate and must be replaced by connective tissue cells which secrete fibers to form **scar tissue.** The lymphocytes are believed to be active in this process, since frequently there are great numbers of them in areas where healing is occurring. Experiments in which lymphocytes are grown outside the body in sterile media have shown that in these conditions, and presumably also inside the body, lymphocytes can change into connective tissue cells and thus facilitate the processes of repair.

A second protection against disease which the body has are **antibodies** (see p. 401), specific protective substances, usually proteins, which are formed in response to some foreign material in the blood stream called an **antigen.** Lymphocytes, and certain other cells of the body, are believed to be responsible for manufacturing these antibodies.

The eosinophils collect in large numbers whenever the body is infected with an animal parasite such as the *Trichinella* worm, which causes trichinosis (see p. 409), and probably are helpful in counteracting such diseases. Eosinophils are usually abundant also during attacks of hay fever, asthma and similar conditions, but their relationship to them is not known.

Most infections cause an increase in the number of white cells which can be detected by the hemocytometer. In appendicitis or pneumonia the white cell count may increase to 20,000 or even more per cubic millimeter. Since the increase is usually proportional to the severity of the infection, successive white counts are used to gauge a patient's recovery. Furthermore, in certain diseases particular kinds of white cells increase in number, so that a differential white count may aid a physician in diagnosing a particular case. The percentage of lymphocytes in the blood is increased in pernicious anemia and whooping cough, by living at high altitudes or in the tropics, and by sun tan. Typhoid fever and malaria usually effect an increase in the percentage of monocytes. A rise in the percentage of neutrophils is characteristic of pneumonia and appendicitis. An increase in eosinophils takes place when the body is infected with some sort of animal parasite, such as a tapeworm or

hookworm, and in scarlet fever, asthma and some skin diseases. A rise in the percentage of basophils is characteristic of leukemia. Some diseases, such as influenza and measles, bring about a decrease in the number of white cells.

7. The Life History of White Cells. Although it has so far been impossible to measure directly the rate of white cell formation and destruction, indirect studies indicate that the normal life span of white cells is between one and four days. White cells contain nuclei, but division does not occur among those in circulation. The different types of white cells originate in different parts of the body: the lymphocytes are formed in the lymph nodes and enter the blood by way of the lymph vessels; the monocytes are formed in the lymph nodes, spleen and perhaps in other organs. The other three white cells originate in the red bone marrow, from cells outside the blood vessels and, when mature, pass through their walls and enter the blood stream. Some investigators believe that these white cells and the red cells originate from a common stem cell.

White cells are not destroyed by any particular organ of the body—some are killed by bacteria in the body's constant battle against them; others wander through the lining of the digestive tract or urinary system and are swept out of the body with the feces or urine.

III. DISEASES OF THE BLOOD

8. Anemia. Anemia is not a specific disease, but a symptom which has many causes. It is characterized by a decrease in the number of red cells in the blood or in the amount of hemoglobin in the red cells, or by both. In an anemic person the red cell count may fall to four, three or or even one million per cubic millimeter. In anemias caused by the excessive loss or destruction of these cells, the red bone marrow tries to compensate by increasing its rate of cell formation, and immature, nucleated red cells are released into the blood stream. Anemias are harmful because they interfere with the transportation of oxygen, thereby impairing cell metabolism, and, if severe enough, lead to the death of the cells and the organism.

One cause of anemia is injury to the organs concerned in the manufacture of red cells—the bone marrow, liver and spleen. Tumors of the red marrow may destroy enough tissue to produce anemia, and certain substances such as benzol and lead are especially destructive of red marrow, so that industrial workers continually exposed to them may acquire the condition.

Any great loss of blood results in temporary anemia until the red marrow can make replacements. The number of red cells in 500 cc. (a pint) of blood (the usual amount taken from a donor in a blood transfusion) is replaced in from one to two weeks. Between two and four weeks are required for the red count to return to normal after the loss of a liter of blood; to lose 2 liters or more is usually fatal, unless transfusions are promptly given.

Anemia frequently accompanies pregnancy because of the demands of the embryo upon the mother's supply of raw materials (chiefly iron) for hemoglobin. The embryo must store up enough iron to carry it

through its first year or so of life when its diet is almost wholly milk. Milk is a poor source of iron, and a prolonged milk diet will cause anemia. Because most of the iron of hemoglobin is salvaged and re-used, the amount needed in the diet is low—about 0.01 gm. daily—and an ordinary diet easily supplies it.

Pernicious anemia, so called because until 1927 it was as uniformly fatal as an advanced case of cancer, is characterized by successive decreases of the red cell count, sometimes with a partial recovery between attacks, until death occurs. The red cells in a person suffering from this disease have a normal hemoglobin content, but are excessively fragile because of a deficiency of the material providing the structural framework of the cell. For this reason the cells are destroyed more rapidly than usual. A clue to a possible treatment of the disease resulted from studies on dogs made by Dr. Whipple at the University of Rochester. The animals were first made anemic by repeated bleedings, then fed various diets, and observed for signs of recovery. Liver was found to be the best food for promoting the normal condition. After these experiments some physicians at Harvard University fed patients suffering from pernicious anemia large amounts of liver. The results were striking: the red cell count began to rise after a few days and reached normal within several weeks. Feeding liver does not effect a cure, however, for if it is stopped, the anemia returns and the patient dies. But as long as he eats sufficient liver to supply the substance necessary for normal cell structure, the red count remains normal, and the patient enjoys almost normal health. A liver extract containing this substance is now available, and people suffering from pernicious anemia can take the extract rather than eat whole liver. In 1948 the substance was isolated and is now known as vitamin B_{12}. In normal persons the chemical is produced in the stomach, and the basic cause of pernicious anemia is any malfunctioning of that organ which prevents its manufacturing the anti-anemia material.

Anemia will result from any condition which destroys red cells—malaria, syphilis, burns and chemicals, and the presence of certain worm parasites. One of the effects of rattlesnake venom is the destruction of red cells. A hereditary defect, sickle cell anemia, is characterized by the production of cells abnormal in shape and so fragile that destruction is excessive.

9. Polycythemia. An increase in the number of red cells—reaching perhaps 15,000,000 per cubic millimeter—is called **polycythemia.** This condition follows diarrhea because of the decreased fluids of the body. The total number of red cells is not increased, but, because there is less plasma and a smaller total blood volume, a temporary increase in the number of red cells *per cubic millimeter* results. Polycythemia may also be effected by an overproduction of the red cells in the red marrow.

10. Leukemia. Leukemia is a disease of the cells giving rise to white cells. They multiply much too rapidly, increasing in number to several hundred thousand per cubic millimeter of blood. The cells produced are abnormal, and many are immature. This disease, usually fatal and of unknown cause, is similar to cancer in that a group of cells suddenly begin to multiply too rapidly.

IV. BLOOD PLATELETS

The third formed element of the blood, the blood platelets, is important in helping to initiate blood clotting. The platelets are tiny (about one third the diameter of a red cell), colorless, spherical bodies without a nucleus. Most of them, it is believed, originate from the breaking off of pieces of giant cells in the red marrow, although recent experiments indicate that some are formed by certain phagocytic cells in the lungs. Their life span is about four days.

11. The clotting of blood. An elaborate mechanism has evolved to prevent accidental loss of blood from the body. In some of the lower animals, such as the crab, excess loss is prevented by the powerful contraction of muscles in the wall of the blood vessel. In man and the other vertebrates this end is accomplished by a series of chemical reactions resulting in a **clot** which plugs the broken vessel. Clotting is essentially a function of the plasma, not of the blood cells, and involves the changing of one of the plasma proteins, fibrinogen, from the sol (liquid) to the gel (solid) state.

When blood is drawn from a blood vessel into a container, it changes from a liquid into a semisolid gel in about six minutes (the clotting time varies from about four to ten minutes). The change in consistency is brought about by the presence of tiny, threadlike structures, which form an interlacing network of fibers, made of a material called **fibrin**. The fibers primarily form in the region of disintegrating platelets, but may appear even in their complete absence. Meanwhile, red and white cells become caught in the meshes of the fibrin network and contribute to the solidity of the clot, although they, too, are unessential for the clotting process. After the clot has formed, it shrinks and squeezes out a straw-colored fluid, **serum**, which does not clot, but remains fluid indefinitely. (It is similar to plasma in most of its constituents, but it differs in lacking fibrinogen, since this substance is removed and changed into fibrin during the clotting process.)

Most people have the erroneous idea that blood clots because it is exposed to air or because it stops flowing. Actually, blood clots in the complete absence of air, and if carefully drawn into a vessel lined with paraffin, it will not clot even though exposed to air. There are several organs in the body, such as the spleen, where blood normally remains stationary for hours at a time without clotting. The clotting process is initiated and accelerated by the juices from injured tissues, by foreign matter, and rough surfaces. When blood is drawn into a glass vessel, the platelets collect on the surface of the glass and disintegrate. If the vessel is lined with paraffin and then filled with blood, the disintegration of the platelets and the clotting of the blood are greatly delayed. When a little juice from injured tissue is added to this, clotting occurs in the normal time. Both injured tissues and distintegrating platelets give off similar substances, collectively called **thrombokinase**, which initiate the clotting reaction. From this it is clear why clotting occurs automatically at the proper time. When blood escapes from an injured vessel, it is immediately exposed to juices from damaged tissue, and its platelets disintegrate, releasing additional thrombokinase.

Serum contains a chemical, called **thrombin,** which, when added to a solution of purified fibrinogen in a test tube, effects the formation of a typical clot. Thrombin is believed to be the immediate factor in the mechanism which changes fibrinogen into fibrin and produces the clot. This chemical does not exist as such in circulating blood, for, since fibrinogen is always present, thrombin would cause clotting inside the blood vessels. Instead, thrombin exists in the blood in an inactive form, **prothrombin,** which is changed by thrombokinase and calcium into thrombin at the time of clotting.

Blood can be prevented from clotting by the addition of sodium oxalate or sodium citrate, which removes the calcium. But calcium is not necessary for the reaction of thrombin with fibrinogen to produce fibrin. Blood has an additional safeguard to prevent clotting from occurring within the blood vessels: prothrombin itself does not occur as such in normal plasma, but is combined with a substance called **antiprothrombin,** with which thrombokinase is believed to unite in order to initiate the clotting mechanism. This union releases the prothrombin.

The clotting process is complex, and some investigators have postulated that additional substances are involved in it. Since thrombokinase and thrombin resemble enzymes in many ways, some specialists believe the process to be enzymatic. It has been demonstrated that the digestive enzyme trypsin causes fibrinogen to change to fibrin. The clotting mechanism is not yet fully understood, but the generally accepted theory is that it occurs in three steps, as follows:

1. Thrombokinase (released from injured tissues and disintegrating platelets) + { Antiprothrombin / Prothrombin (present in the plasma in chemical union) } ⟶ Prothrombin + { Antiprothrombin / Thrombokinase }

2. Prothrombin + Calcium (present in normal plasma) ⟶ Thrombin

3. Thrombin + Fibrinogen (soluble protein present in normal plasma) ⟶ Fibrin (insoluble protein which constitutes the actual clot)

Some bacteria, notably those causing syphilis, attack and destroy the walls of blood vessels, and it is a secondary function of the clotting chemicals to aid in the repair of such weak spots. The destruction of the cells and the accumulation and distintegration of platelets on the roughened wall liberate thrombokinase and cause the formation of a clot across the weakened area. The clot alone is not very effective, but connective tissue cells from the arterial wall migrate in and secrete tough, fibrous connective tissue (scar tissue) to reinforce the clot. The danger of the clotting mechanism lies in the fact that the clot inside the vessel (called a **thrombus**) may grow completely across the cavity and prevent blood from passing. Many organs have several blood vessels supplying them, and in these a thrombus is not dangerous. In others, served by a single vessel only, a thrombus can be fatal. Sometimes a thrombus formed in some unessential vessel breaks loose and is carried

by the blood to some other vessel, which it obstructs. A thrombus or any other particle carried by the blood stream which blocks a blood vessel is called an **embolus.**

Prothrombin is believed to be manufactured by the liver, and diseases of that organ may interfere with this and produce defective clotting. For the manufacture of prothrombin, an adequate supply of vitamin K is necessary. Since bile is required for the absorption of vitamin K from the intestine into the blood, a deficiency of bile may produce a deficiency of prothrombin and hence defective clotting, even if the diet contains an adequate supply of vitamin K. Surgical operations on the liver or bile duct in the past were often followed by internal hemorrhages, but patients are now treated with injections of vitamin K.

The blood which flows during menstruation (see p. 326) does not coagulate, either because its fibrinogen has been removed by the lining of the uterus, or because it has already clotted and its fibrin has been destroyed by proteolytic enzymes. It has been reported that circulating blood contains less prothrombin at this time and that the clotting time is increased.

The hereditary disease **hemophilia,** which affects males and is transmitted to them by the maternal parent, is characterized by clotting so defective that a slight scratch may cause a fatal hemorrhage. It has attracted wide attention because it was present in several of the European royal families, notably the Bourbons of Spain and the Romanoffs of Russia. The exact nature of the defect is unknown. The number of platelets and the amounts of calcium, fibrinogen and prothrombin in the blood of a hemophiliac are normal. Furthermore, the platelets are unusually stable, and thus do not disintegrate readily when blood is shed. This has suggested the theory that the defective clotting depends on the failure of the platelets to disintegrate and release thrombokinase to set off the chain of reactions leading to clotting. Another theory is that the blood of hemophiliacs contains a substance which destroys thrombokinase or renders it inactive as fast as it is released.

The clotting property of plasma has made it an important tool in tissue-culture research. After several unsuccessful attempts to grow tissues outside the body, Dr. Ross Harrison succeeded in 1910 when he used a drop of plasma as a medium for the tissue. The plasma clots and provides a necessary foundation for the cells to grow on. This discovery provided a technique by means of which much research has been done on the growth, development and fundamental properties of tissues, bacteria and viruses.

V. MEDICO-LEGAL TESTS FOR BLOOD

If you are a detective story fan, undoubtedly you have read of detectives submitting suspicious, brown stains for police laboratory analysis, and, upon learning that they are human blood, arresting their suspects. You may have wondered how blood stains can be identified positively. The simplest test for blood consists in adding to a stain some benzidine (a common organic reagent) and hydrogen peroxide (the familiar bleaching agent): if hemoglobin is present in the stain, it turns green.

But this is a test for hemoglobin only and does not distinguish human from other blood.

An extremely delicate test, which can detect one part of blood when it is mixed with more than a million parts of other materials, makes use of a chemical known as 3-aminophthalhydrazide. This substance, plus sodium hydroxide and hydrogen peroxide, is added to a stain, and if blood is present, a blue, phosphorescent light is given off. Even after a blood stain has apparently been removed by repeated washings, so that no trace is visible, this test will reveal the location of the spot because of the minute amount of hemoglobin invariably remaining.

To distinguish human from other blood, the precipitin test is used. This depends upon an **antigen-antibody** reaction. An antigen is defined as any foreign protein which is introduced into the blood stream and causes the blood to respond by manufacturing an antibody which will react specifically with it. In preparing for the test, human serum (containing one or more proteins characteristic of man which act as antigens) is injected into a rabbit, over a period of time, until 30 cc. have been injected. The white cells of the rabbit are stimulated by the presence of the antigen (the human serum protein) to manufacture antibodies which will react specifically with human serum. After a lapse of five days the rabbit is bled, and the serum extracted and kept until needed. In making the test, a solution containing the suspected material is prepared and mixed with the rabbit serum, since the latter is known to contain antibodies for human serum. If the suspected material contains human blood, and therefore human serum antigens, the antibodies and antigens react and cause a precipitation which appears in from one to three hours. If the suspected material contains some other kind of blood only a slight precipitation or none at all occurs. If the blood is from an animal closely related to man—say a chimpanzee—a slight precipitation results; the blood of a more distant relative causes an even slighter reaction.

VI. BLOOD TYPES AND TRANSFUSIONS

The practice of injecting or transfusing blood from an animal or man into a person suffering from its lack is not new, having first been attempted in 1667. Transfusions between animals and men were usually unsuccessful, evoking severe reactions and often death. But the transfusion of blood from one human being to another was sometimes successful, although occasionally a clumping or agglutination of the patient's red cells resulted. Agglutination is caused by an antigen-antibody reaction and must be carefully distinguished from coagulation, the clotting of blood caused by the thrombin and fibrinogen reaction.

The mystery of why transfusions were sometimes unsuccessful was solved by Landsteiner, in 1900, who found that human blood may differ chemically from person to person, and that when the bloods of donor and patient are incompatible because of these chemicals, agglutination is the result. There are four main blood groups, **O**, **A**, **B** and **AB**, distinguishable by the presence of agglutinogens (a type of antigen) A or B in the red blood cells, and by agglutinins (a type of antibody) a or b

in the plasma. Table 4 summarizes the agglutinogens and agglutinins in the different blood groups and shows which transfusions are possible. Normally, no blood agglutinates itself, because the corresponding agglutinogen and agglutinin (A and a, for example) are not present together.

Table 4. The Human Blood Groups

Blood Group	Agglutinogen in Red Cells	Agglutinin in Plasma	Can give Blood to Groups	Can Receive Blood from Groups
O	None	a and b	O, A, B, AB	O
A	A	b	A, AB	O, A
B	B	a	B, AB	O, B
AB	A and B	None	AB	O, A, B, AB

In actual practice the physician makes every effort to find a donor of the same blood group as the patient and, if circumstances permit, a direct test is made by mixing serum from the patient with some corpuscles from the prospective donor, to make sure they are compatible. Besides the four main groups, there are two subgroups which must also be taken into consideration. In an emergency, if no donor of the patient's type is available, blood of another type may be used, provided that the serum of the patient does not agglutinate the corpuscles of the donor. For example, a type B person may receive blood from a type O donor, because the O red corpuscles have no agglutinogens and thus will not be clumped by any kind of plasma. The agglutinins present in the O serum are mixed with the patient's serum and so diluted that they do not cause his red corpuscles to clump. Type O people are called "universal donors," because their blood can be given safely to any person, and type AB people are known as "universal recipients," since they can receive blood of any type. The blood groups are inherited (see p. 441), and remain constant throughout life.

A blood type is determined by mixing a sample of it with serum of a known blood type. The serum of type A blood contains the b agglutinin, and will cause the clumping of any red cells containing B agglutinogens. In performing the test, a clean glass slide is marked with two circles, labeled A and B; a drop of serum from a person known to have type A blood is placed in one circle, and a drop of B serum is placed in the other. Then a drop of blood from the person being tested is added to each kind of serum and mixed. If clumping is to occur, it does so within two or three minutes and is visible to the naked eye. It is even possible to detect the type of a small blood stain, and such tests have sometimes been important in murder cases.

Blood tests have been given to persons of practically all races, and some marked differences have been found. No one blood type characterizes a single race exclusively, however; racial differences lie in the relative frequency of the blood types. Because one's blood type is inherited and there can be no conscious selection of mates for certain blood types, knowledge of them is an important tool in anthropology. The proportions of the groups in a population remain constant from generation to generation, as long as there is no intermarriage with other

people. The work of Verzár and Weszeesky in Hungary reveals an interesting example of this. Gypsies, who originally eame from India, have lived in Hungary for several hundred years, but beeause there has been little mating between them and native Hungarians, the distribution of their blood groups is similar to that of the Hindus, and quite different from that of the Hungarians. The Germans who migrated to Hungary about 1700 have kept, in addition to their German language and eustoms, a blood group frequeney charaeteristic of Germans in Germany. With the diseovery of teehniques for determining the blood types of mummies and skeletons, the use of blood tests in anthropology was eonsiderably broadened. Candela tested the blood types of thirty prehistorie Aleutian mummies and found eight of them to be group B or AB. Previously, the Aleuts were thought to be the result of an Eskimo-Indian eross, but both Eskimos and Indians have a low pereentage of B and AB groups, whereas B is common in Asia. These findings, indieating that the Aleuts were of Asiatie origin, have been substantiated.

Other, independent blood types, whieh provide an additional means of identifying blood, depend upon the presenee in the red eells of entirely different agglutinogens, ealled **M** and **N**. These are inherited independently of the previous blood groups, so that a person may be both A and M.

A third set of hereditary faetors eauses the presenee or absence of another agglutinogen, the **Rh factor,** so ealled because it was first found in the blood of rhesus monkeys. About 85 per eent of white people are Rh positive, about 15 per eent Rh negative. This Rh factor plays an essential role in a frequently fatal type of anemia of the newborn, *erythroblastosis fetalis.* If the mother is Rh negative, the father Rh positive, and the developing embryo is Rh positive (having inherited this factor from the father), blood from the fetus may pass across some defect in the placenta and stimulate the formation of Rh positive antibodies by the white eells of the mother. When the mother beeomes pregnant a second time, some of these antibodies may pass through the placenta into the ehild's bloodstream and cause the destruction of its red eells. In extreme cases, so many red eells are destroyed that the embryo dies before birth, but more frequently it is born alive and dies soon afterwards. In other cases the destruetion of red cells is not so extensive and the infant reeovers.

Blood groups have also been demonstrated in apes, monkeys, sheep, dogs, eats, horses, rabbits, pigs, pigeons, chiekens, mice and rats. Groups O and A have been found in ehimpanzees, groups A, B and AB in orang-utans, and groups A and B in gorillas. The presence of these groups among the apes and monkeys indicate that the blood group substanees arose before the primates had finally evolved into different types. Substanees similar to, but not identical with, the human A and B substanees have been demonstrated in the blood of many different mammals and birds. M and N agglutinogens, similar to those of man, have been found in ehimpanzees, orang-utans and some monkeys, but not in any other animals. The M and N substanees of the ehimpanzees are most like those of man, confirming the generally aeeepted idea that chimpanzees are the most manlike of the anthropoid apes.

The transfusion of whole blood and plasma plays an extremely important part in saving lives. After a proper donor has been selected, care must be taken, first, to prevent the coagulation of the transfused blood (sodium citrate, which removes calcium ions and thus prevents coagulation, is usually added), then to prevent infection, and finally to introduce the blood into the patient's vein at the proper temperature and rate. If too much blood is injected at one time, the heart will be overloaded. Recently, methods have been devised for storing citrated blood as long as thirty days, making "blood banks" possible in many hospitals. Usually, a patient requiring a transfusion is given blood of the proper type from the bank, and the supply is replenished later by blood of any type from a member of his family. In this way the expense of blood from a professional donor is eliminated. The blood is stored in a refrigerator kept at 4° to 6° C.

The transfusion of substitutes for whole blood dates back to 1878, when cow's milk was used experimentally. Recently, plasma and serum, which can be stored longer than whole blood, have frequently been substituted for it. Both contain the plasma proteins which do not diffuse through the blood vessel walls, and so are useful in the treatment of shock. However, both are good culture media for bacteria and molds, and extreme care must be taken to collect, treat and store the substances under sterile conditions. With the recent development of methods for drying plasma by freezing it, and removing the water under vacuum, this danger has been obviated. Dried plasma in a sealed sterile container will keep without refrigeration for a long time. When it is to be used, it is mixed with the proper quantity of sterile, distilled water and injected. An additional advantage is that it can be given to a person of any blood type. In practice, the bloods of sixteen different persons of assorted blood types are pooled, so that the different agglutinins are diluted below their effective concentration and will not affect the red cells of the patient's blood.

QUESTIONS

1. Name seven functions of blood. Which is the most important?
2. How are these functions carried on in animals which do not have a circulatory system?
3. Distinguish between plasma, serum, lymph and tissue fluid.
4. What is oxyhemoglobin? What is its significance in the body?
5. Why is carbon monoxide poisonous?
6. Where and how are red cells manufactured?
7. Why does the number of red blood cells increase at high altitudes?
8. What are the chief structural and functional differences between white blood cells and red blood cells?
9. Describe how clotting occurs. What prevents it from occurring at any time within the blood vessels?
10. What is agglutination?

SUPPLEMENTARY READINGS

Haden, R. L.: *Principles of Hematology*. 3rd ed. Philadelphia, Lea & Febiger, 1946.
A detailed description of blood cells and their functions.

Weiner, A. S.: *Blood Groups and Transfusions*. 3rd ed. Springfield, Ill., Charles C Thomas, 1943.
An interesting account of blood groups and the use of blood-grouping technique in anthropological investigations.

CHAPTER 9

THE CIRCULATORY SYSTEM

BECAUSE it carries food and oxygen to all the tissues of the body, and removes the waste products of metabolism, the circulatory system is frequently called "the transportation system." It is also important in equalizing body temperatures. For these purposes, then, it includes the heart, the blood vessels and the lymph vessels, in addition to the blood itself. To understand how the system operates as an integrated unit, we must first study the structure and function of each of the organs involved.

I. THE BLOOD VESSELS

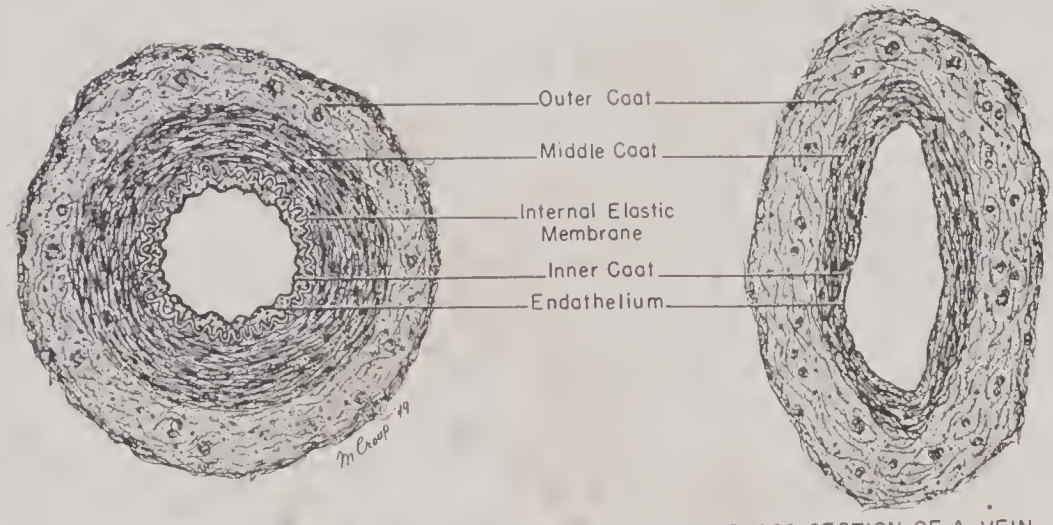
There are three types of blood vessels: *arteries, veins* and *capillaries*. Arteries and veins are distinguished from each other by the direction of the flow of blood in them, not by the kind of blood (acrated or nonaerated) which they contain. Arteries carry blood from the heart *to* the tissues of the body; veins return blood *from* the tissues to the heart. Capillaries are microscopic vessels located in the tissues, connecting the arteries and veins. Their chief function is to effect the exchange of food, gases and wastes between the blood and the tissues. To do this, they have extremely thin walls consisting of a single layer of cells, the endothelium, which is continuous with the endothelial lining of the artery and vein on either side (Fig. 67, *C*). Some capillaries are so small that the red corpuscles are bent in passing through them.

The walls of arteries and veins are too thick to permit diffusion, being made of three distinct layers: an **outer** coat of connective tissue, a **middle** coat of smooth muscle cells, and an **inner** coat of endothelium and connective tissue (Fig. 67, *A*). The outer coat contains many elastic fibers which make the artery tough and resistant to internal pressures, while permitting it to expand and then contract each time the heart beats. The smooth muscle in the middle layer regulates the amount of blood going to a particular organ by contracting or relaxing, and so decreasing or increasing the size of the lumen (cavity) of the artery. In addition to the endothelial lining, the inner coat of most arteries contains a strong **internal elastic membrane** to give additional strength to the walls. The arterial walls are also supplied with two sets of nerves; impulses carried by one set cause the smooth muscles to contract, those carried by the other set effect a relaxation. The largest artery, the **aorta**, is about an inch in diameter near the heart, and has a wall about ⅛ inch thick.

Although the walls of veins are much lighter and thinner than those of arteries, they have the same three coats (Fig. 67, *B*). The outer one of connective tissue has fewer elastic fibers, the middle muscular layer is thinner than the corresponding arterial layer, and in most veins there

is no internal elastic membrane. Veins, but not arteries, are supplied with valves along their length to prevent the baek-flow of blood.

The eells of the body are surrounded by and bathed in a liquid ealled **tissue fluid,** and blood does not eome in direet eontaet with them. Instead, substanees must diffuse from the blood, through the wall of a capillary, and across the space filled with tissue fluid to get to the eells (Fig. 68). The faet that the capillaries are small means that eaeh drop of blood passing through a eapillary network is exposed to a large surfaee area through whieh diffusion may oeeur. It has been estimated that



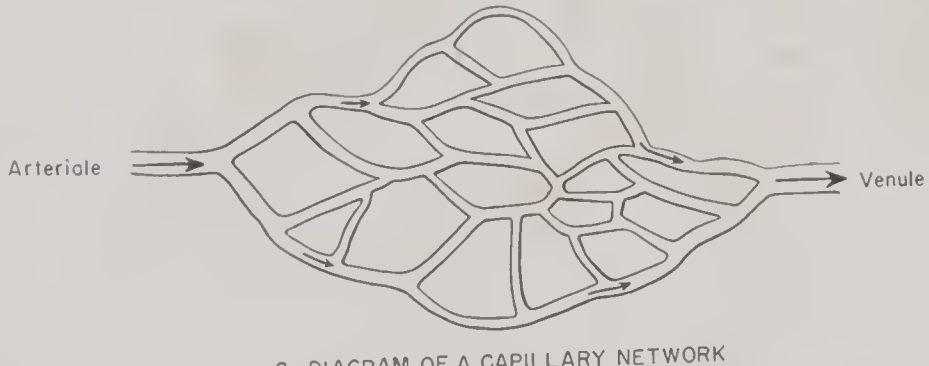


Fig. 67. Arteries and veins compared.

each cubie eentimeter of blood is exposed to 7000 square em. or about 8 square feet of capillary surfaee. The number of eapillaries in the body is almost beyond ealeulation. In tissues sueh as musele, with a high metabolie rate, they are elose together, the distanee between adjaeent ones being about twice the diameter of the capillary (Fig. 68). One investigator plaees the number of eapillaries in muscle tissue at about 1,500,000 per square inch. Less aetive tissues are not so well supplied—fatty tissue has few eapillaries, and the lens of the eye has none at all. Ordinarily, only a fraction of the eapillaries of any organ are filled with blood and functioning, but during periods of intense aetivity, all, or nearly all, the eapillary networks are full.

II. THE HEART

The heart is a powerful muscular organ located in the chest directly under the breast bone. Its walls are made of cardiac muscle tissue held together by strands of connective tissue. Enclosing it is a tough, connective tissue sac (the pericardium). The inner surface of this sac and the outer surface of the heart are covered by a smooth layer of epithelial-like cells, and the cavity contains a fluid, reducing friction to a minimum as the heart beats.

The muscle fibers branch and fuse to form a complex network of protoplasmic connections throughout the heart wall, across which nerve impulses can travel. Because of this, the heart contraction follows the "All-or-None" Law (see p. 258); that is, if a nerve impulse is sufficiently strong to make the heart beat at all, it responds with a maximum contraction. The heart and all the blood vessels are lined with a layer of

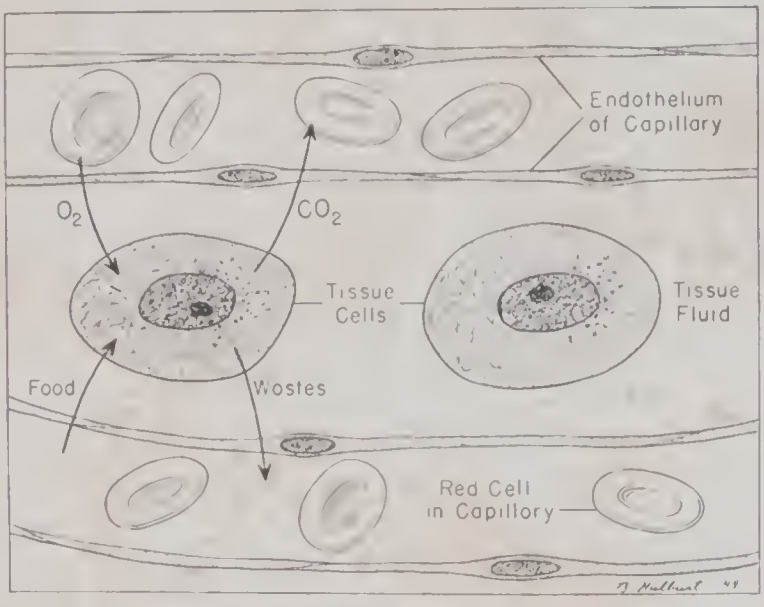


Fig. 68. Diagram of the diffusion of materials between capillaries and the cells of the body, by way of the tissue fluid which bathes the cells.

smooth, thin cells, the **endothelium**, which prevents blood from clotting within the circulatory system. Any disease or injury of the endothelium which roughens it may cause the formation of a thrombus within the vessel.

The heart of man and other mammals and of birds is divided into four chambers (Fig. 69), the upper right and left **auricles**, and the lower right and left **ventricles**. The auricles, which have relatively thin walls, receive blood from the veins and push it into the ventricles. The latter, with much thicker walls, pump the blood out of the heart and around the body.

For its function as a pump, the heart is supplied with valves that close automatically to prevent blood from flowing in the wrong direction. There is an opening for blood to pass from the right auricle to the right ventricle, and a second opening from the left auricle to the left ventricle, but no connection between right and left auricle or right and left ventricle. The heart is really two separate pumps, then, sometimes called the right heart and the left heart. The valve between the right auricle and ventricle, with three flaps or cusps, is called the **tricuspid**

valve. That between the left auricle and ventricle, with only two cusps, is called the **biscuspid** valve. These two valves are held in place and prevented from being pushed back into the auricles when the ventricles contract, by stout cords or "heartstrings" attached to the valves and the walls of the ventricles (Fig. 69). At the bases of the two big arteries—the pulmonary and the aorta—which leave the right and left ventricles, respectively, are additional flaps of connective tissue, the two **semilunar** valves, so called because of their half-moon shape. These are really pouches opening away from the heart. When blood passes in the proper direction, the pouches are pushed aside and offer no resistance. But when the ventricles are relaxing and filling with blood, and the blood

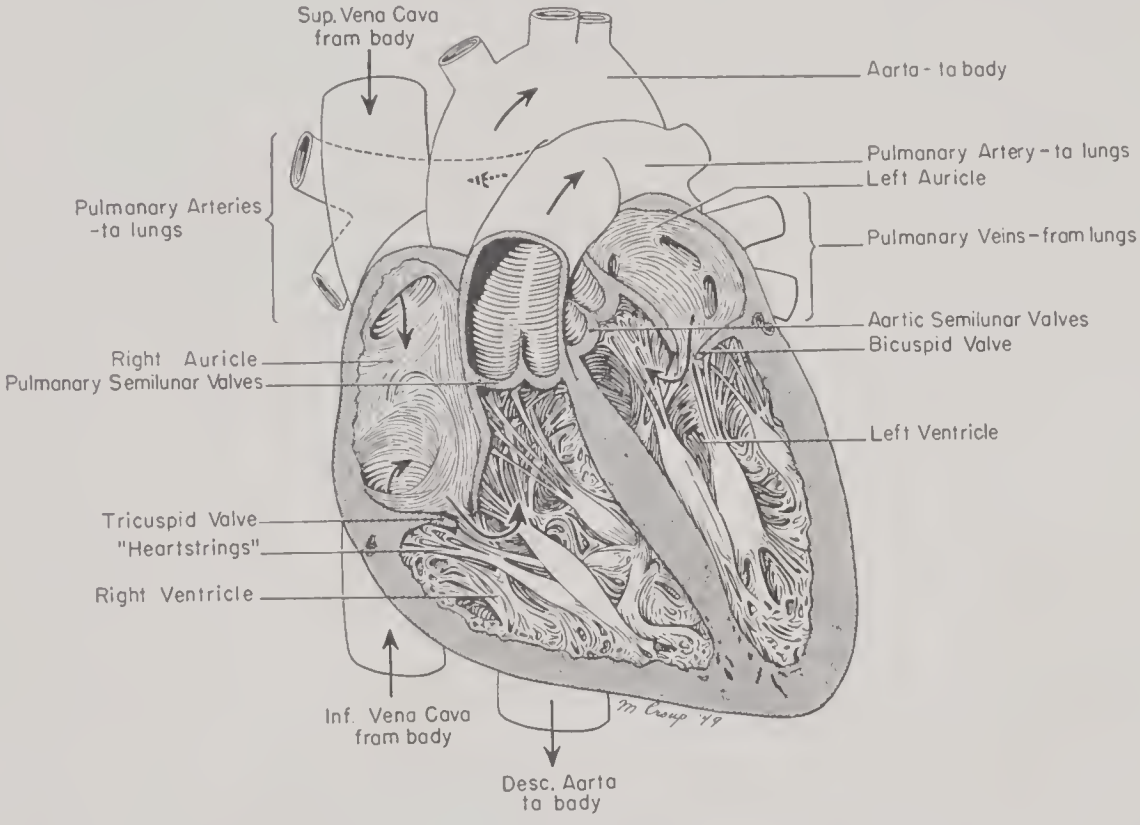


Fig. 69. Diagram of the heart, showing chambers, valves and connecting vessels.

pressure in the arteries is higher than that in the ventricles, blood fills the pouches, causing them to stretch across the cavity of the pulmonary artery or aorta, and thus prevent a leakage back into the heart (Fig. 70).

Because there is no valve at the openings of the large veins leading into the right auricle, or at the openings of the pulmonary veins into the left auricle, some blood is forced back into the veins when the auricles contract. This is less than it might be because of rings of muscle tissue around the veins in that region, which contract just before the auricles do.

The right auricle receives blood from all parts of the body (except the lungs) by way of two large veins: the **superior vena cava,** which drains the head, arms and upper part of the body, and the **inferior vena cava,** which drains the legs and the lower part of the body. The walls of the left ventricle are thicker than those of the right one because more

force must be exerted to push the blood through the body than to push it to the lungs.

The path of blood through the heart may be summarized as follows (Fig. 69): blood from the body enters the right auricle, the contraction of which pushes open the flaps of the tricuspid valve, pumping the blood into the right ventricle. The contraction of the right ventricle then closes the tricuspid valve, opens the semilunar valve, and pushes blood out via the pulmonary artery to the lungs. Blood returning from the lungs in the pulmonary veins enters the left auricle, and is pumped by its contraction through the bicuspid valve into the left ventricle. The contraction of the left ventricle closes the bicuspid valve, opens the semilunar valve, and sends the blood out the aorta to all parts of the body. Every drop of blood entering the right auricle must go through

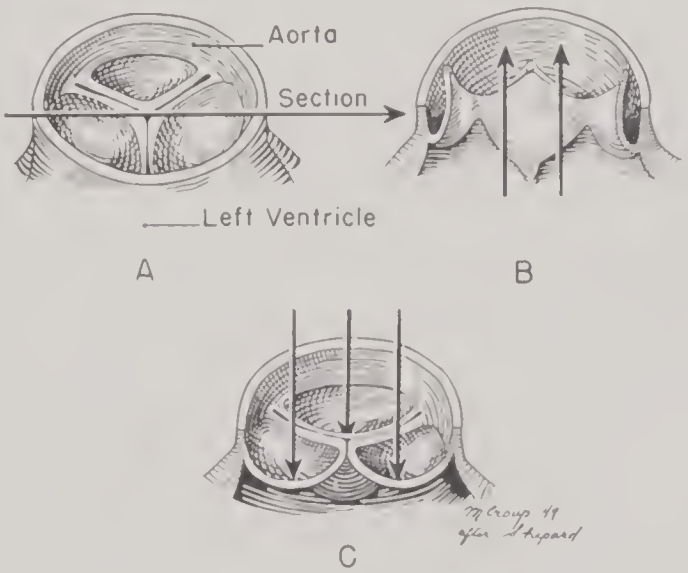


Fig. 70. Diagram of the operation of the semilunar valves. *A*, Arrangement of the three pouches of the semilunar valves. The aorta has been cut across just above its point of attachment to the ventricle, to expose the valves. *B*, When the ventricle contracts, the expelled blood (indicated by arrows) pushes the pouches aside and passes into the aorta. *C*, When the ventricle relaxes, blood from the aorta fills the pouch (arrows), causing them to extend across the cavity and prevent the leakage of blood back into the heart.

the lungs before it can get into the left ventricle and be pumped around the body.

The heart muscle is not, as one might assume, nourished by the blood within its chambers, because its walls are too thick for food and oxygen to diffuse through. Instead, it is supplied with blood by arteries spreading over its surface, which branch off the aorta, at the point where that vessel leaves the heart. Veins from the heart tissue drain into the right auricle, except for a few small veins which drain from the heart wall directly into the ventricle.

1. The Heart Beat. Beating is an inherent capacity of the heart, exhibited early in embryonic development and continuing without pause throughout life. Since all tissues need a constant supply of oxygen which the circulating blood provides, unconsciousness results if the heart stops beating for a few seconds, and death ensues if it stops for a few minutes. The heart of a resting human being pumps about 5 liters of blood per minute, or about 75 cc. per beat. This means that a quantity of blood

equal to the total amount contained in the body passes through the heart eaeh minute. Not all the blood aetually goes through the heart once a minute: some of the blood on the shorter eireuits will have been through more than onee, while that on the longer eireuits will not yet have passed through. In man's three seore and ten years, his heart beats about 2,600,000,000 times, and pumps at least 155,000,000 liters (about 150,000 tons) of blood. Estimates of the work done by the heart indicate that it is enough to raise a weight of 10 tons to a height of 10 miles—a truly remarkable performance for an organ that weighs approximately 11 ounees! During exereise both the number of beats per minute and the amount of blood pumped per beat are greatly inereased. Physical training enables the heart to inerease its volume per beat, making it possible for the athletc to inerease the total blood pumped, without as great inerease in the heart rate as would be necessary in an ordinary person.

The faet that the heart eontinues to beat normally after its nerves have been severed shows that it is not dependent upon stimuli from the brain. If kept in the proper liquid medium, it will beat even when entirely removed from the body. Even a few musele fibers disseeted from the heart retain this ability. The rate of the fundamental, innate eontraetion is regulated by a number of faetors—the **nodal tissue** within the heart, and two sets of nerves from the brain.

Nodal Tissue. Nodal tissue, whieh is peeuliar to the heart, instigates and regulates its beat. It has some of the properties of musele and some of nervous tissue. In the lower vertebrates, sueh as fish and frogs, there is a separate chamber of the heart, the **sinus venosus,** into whieh the veins empty, and whieh in turn passes blood to the right auriele. In higher forms this has disappeared except for a vestigial mass of nodal tissue called the **sino-auricular node,** or S.A. node, located at the point where the superior vena cava empties into the right auriele (Fig. 71). A second node, lying between the auricles just above the ventrieles, is known as thc **auriculoventricular,** or A.V., node. From the latter a bundle of branching fibers passes down and invades all parts of the ventrieles. Investigators have demonstrated that the sino-aurieular node initiates the heart beat and regulates its rate of eontraetion. For this reason it is called the **pacemaker.** At regular intervals a wave of eontraction sprcads from thc sino-aurieular node through the auricular musele. When it arrivcs at the auriculoventrieular node, the impulse is transmitted to the ventrieles by the bundle of nodal tissue. There is no museular eonncetion between the auricles and ventrieles; their beating is corrclated solely by the speeialized nodal tissue, which eonduets impulses about ten times as fast as ordinary muscle does (the rates are approximately 5 meters, and 0.5 meter per seeond, respeetively). Conduetion by the nodal tissue insures that all parts of the ventriele eontract almost simultaneously. If eonduetion in the ventrieles were by way of ordinary musele tissue, the museles near the base of the ventrieles would contraet first, causing the uncontraeted apex to bulge, and possibly injuring it.

That the sino-auricular node regulates the rate of the heart beat is demonstrated by the fact that warming the node results in an inereased

rate, while cooling it causes a decreased rate. Heat and cold usually have similar effects on other physiological reactions, but heating or cooling other parts of the heart does not affect the rate of its beat. The acceleration of the beat accompanying fever is caused by the stimulation of the sino-auricular node by the warmer blood. When the sino-auricular node is destroyed by injury or disease, the auriculoventricular node takes over its function as pacemaker.

Each heart beat consists in contraction, or **systole,** of the heart muscle followed by its relaxation, or **diastole.** At the normal rate of seventy beats per minute, each complete beat occupies about 0.85 second. The auricles and ventricles do not contract simultaneously: auricular systole* occurs first, occupying about 0.15 second, followed by ventricular systole, which takes approximately 0.30 second. During the other 0.40 second all chambers rest in the relaxed state.

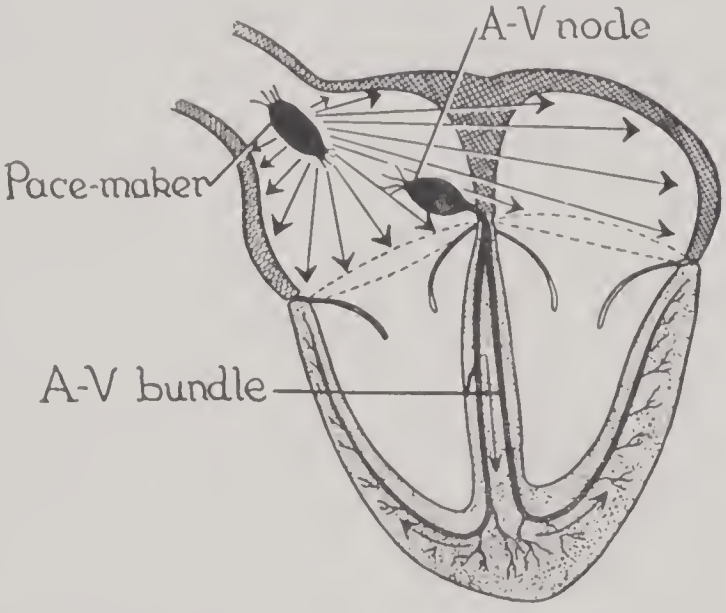


Fig. 71. Diagram of the heart, showing the location of the nodal tissue which coordinates the beating of the various parts. (Reproduced by permission from The Body Functions, by R. W. Gerard, published by John Wiley & Sons, Inc., 1941.)

2. The Heart Cycle. The action of the heart in pumping blood follows a cyclical pattern. For purposes of clarity, we shall follow the successive stages beginning with auricular systole, when the auricles are full of blood.

(*a*) Auricular systole. At this time (Fig. 72, *A*) a wave of contraction, stimulated by the sino-auricular node, spreads over the auricles, forcing blood into the ventricles. The ventricles are already partly filled with blood, owing to the fact that the pressure is lower there than in the auricles, and the tricuspid and bicuspid valves are open. The conduction of the contraction impulse through the auriculoventricular node is slower than in other parts of the nodal tissue, thus accounting for the brief pause after auricular systole before ventricular systole begins.

(*b*) Beginning of ventricular systole (Fig. 72, *B*). The muscles of the ventricular wall, stimulated by the impulse carried by the bundle of

* Even the right and left auricles do not contract exactly at the same time. Because the sino-auricular node is located in the right auricle, where the wave of contraction begins, the right auricle contracts a little before the left auricle does.

nodal tissue from the auriculoventricular node, begin to contract, causing a rapid increase of pressure in the ventricles. The bicuspid and

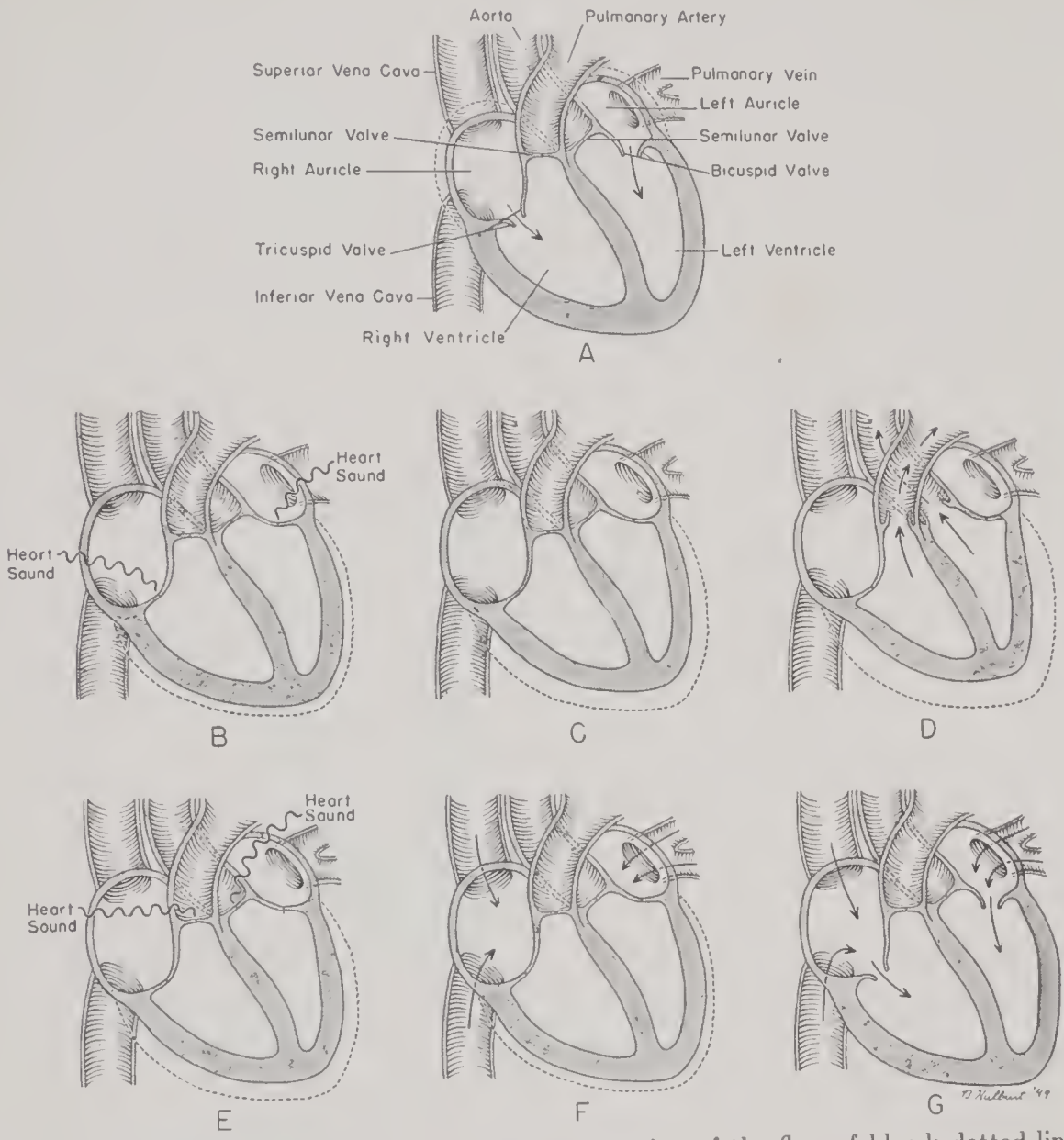


Fig. 72. The heart cycle. Arrows indicate the direction of the flow of blood; dotted lines indicate the change in size as contraction occurs. *A*, Auricular systole; auricles contract, blood is pushed through the open tricuspid and bicuspid valves into the ventricles. The semilunar valves are closed. *B*, Beginning of ventricular systole; ventricles begin to contract, pressure within ventricles increases and closes the tricuspid and bicuspid valves, causing the first heart sound. *C*, Period of rising pressure. Until the pressure within the ventricles equals that in the arteries, the semilunar valves remain closed, and no blood flows in or out of the ventricles. *D*, The semilunar valves open when the pressure within the ventricles exceeds that in the arteries, and blood spurts into the aorta and pulmonary artery. *E*, Beginning of ventricular diastole. When the pressure in the relaxing ventricles drops below that in the arteries, the semilunar valves snap shut, causing the second heart sound. *F*, Period of falling pressure; ventricles continue to relax, and the pressure within them decreases. The tricuspid and bicuspid valves remain closed because the pressure in the ventricles is still higher than the pressure in the auricles. Blood flows from the veins into the relaxed auricles. *G*, The tricuspid and bicuspid valves open when the pressure in the ventricles falls below that in the auricles, and blood flows into the ventricles.

tricuspid valves close immediately, producing part of the first heart sound.

(*c*) Period of rising pressure (Fig. 72, *C*). The pressure in the ventricles mounts rapidly, but until it equals the pressure within the arteries, the semilunar valves remain closed and no blood flows into or out of the ventricles.

(*d*) The semilunar valves open (Fig. 72, *D*). When the intraventricular pressure exceeds that in the arteries, the semilunar valves open and blood spurts into the pulmonary artery and aorta. As the ventricles complete their contraction, blood is ejected more slowly until it finally stops. Ventricular diastole then follows.

(*e*) Beginning of ventricular diastole (Fig. 72, *E*). As the ventricles relax, the pressure within them decreases until it is less than the pressure within the arteries, and the semilunar valves snap shut. This causes the second heart sound.

(*f*) Period of falling pressure (Fig. 72, *F*). After the semilunar valves close, the ventricular walls continue to relax, and the pressure within the ventricles continues to decrease. The tricuspid and bicuspid valves, which closed during the previous ventricular systole, remain closed because the pressure within the ventricles is still greater than that within the auricles. No blood is flowing into or out of the ventricles at this time, although some blood is flowing from the veins into the relaxed auricles.

(*g*) Opening of the bicuspid and tricuspid valves (Fig. 72, *G*). The continued relaxation of the ventricular walls finally lowers the intraventricular pressure below the pressure within the auricles. At that moment the tricuspid and bicuspid valves open, and blood flows rapidly from the auricles into the ventricles. No contraction of the heart causes this; it is due simply to the fact that the pressure within the relaxed ventricle is lower than that of the auricles and veins. Half the volume of the ventricles may be filled before the auricles undergo systole.

The Heart Sounds. The beating heart produces characteristic sounds which can be heard by placing the ear against the chest or by using a stethoscope, an instrument which magnifies sounds and conducts them to the ear. In most normal people, two sounds are produced per heart beat, one of which is low-pitched, not very loud, and of long duration. This is caused partly by the closure of the tri- and bicuspid valves and partly by the contraction of the muscle in the ventricle (all muscles make a noise when they contract). The first sound, which marks the beginning of ventricular systole, is followed quickly by a second which is higher pitched, louder, sharper and shorter in duration. It is the result of the closure of the semilunar valves and marks the end of ventricular systole. The two sounds have been described by the syllables "lubb-dup," and their quality indicates to the physician the state of the valves. When the semilunar valves are injured, a soft hissing noise ("lubb-shhh") is heard in place of the second sound. This is known as a heart murmur and may be caused by syphilis, rheumatic fever or any other disease which injures the valves and prevents their closing tightly, so that blood can leak back from the arteries into the ventricles during diastole. Damage to the bicuspid or tricuspid valve affects the quality of the first heart sound.

3. Electrical Changes in the Heart. When any tissue becomes active—

when a muscle contracts, a gland secretes, or a nerve conducts an impulse—it becomes electrically negative with respect to the surrounding tissues; that is, the active tissue acts as the negative pole and the resting tissues as the positive pole of a battery. These slight **action currents**

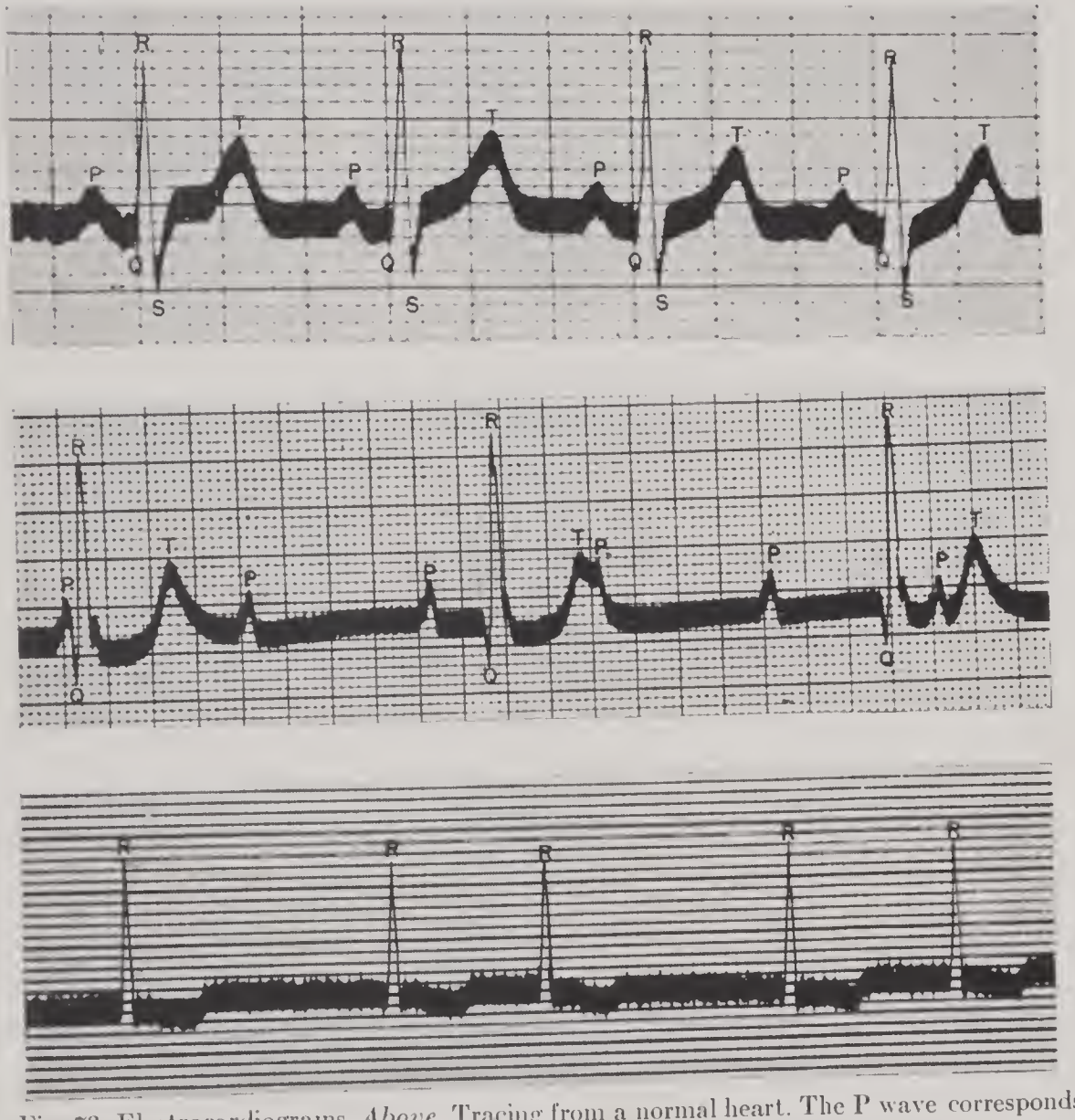


Fig. 73. Electrocardiograms. *Above,* Tracing from a normal heart. The P wave corresponds to the contraction of the auricles, the QRS complex to the contraction of the ventricle, and the T wave to the relaxation of the ventricle. Each heart cycle is marked by P, QRS, and T waves. *Middle,* Tracing from a man with a complete block of the auriculoventricular node, so that the auricle and ventricle are beating completely independently, each at its own rate. Note that P waves appear at regular intervals, and QRS and T waves appear at regular but longer intervals, but that there is no relation between the P and the QRS waves. *Below,* Tracing from a man with auricular fibrillation. Here the individual muscle fibers of the auricle are twitching rapidly and independently, so that there is no regular auricular contraction and hence no P wave. The ventricle beats independently and irregularly, causing the QRS wave to appear at irregular intervals. (Courtesy of Dr. Lewis Dexter and the Peter Bent Brigham Hospital, Boston.)

can be detected with sensitive devices. Those accompanying each beat of the heart are detectable even at the surface of the body by means of an **electrocardiograph,** which records them as a complex, curved line (Fig. 73). Since malfunctioning of the heart causes peculiar action currents, the line recording a pathologic condition will be unusual, and a

trained person can interpret the curves and diagnose the particular abnormality.

4. Adaptation of the Heart Beat to Body Activity. Active tissue requires several times as much oxygen and nutrients as the same tissue at rest, and both the heart and blood vessels are active in the adjustments necessary to provide whatever is needed. During periods of intense exercise the heart can pump seven or eight times as much blood as normal, by increasing the number of beats per minute, or by increasing the blood volume per beat. The heart normally pumps about 70 cc. of blood per beat, but, at maximum, it can pump as much as 200 cc. The following stimuli, singly or together, can effect this increase:

(*a*) A rise in the carbon dioxide content of the blood. During exercise, oxidation occurs more rapidly, and the greater amount of carbon dioxide in tissues and blood stimulates the heart to increase the volume per beat.

(*b*) Stretching of the heart muscle. During exercise the pressure in the veins is higher and more blood flows into the heart chambers before they contract, causing the muscular walls to stretch. The contractile power of a muscle, within limits, is increased by the tension it is under when it begins to contract; hence the greater the volume of blood in the heart at the beginning of systole, the greater will be the quantity of blood pumped per heart beat.

An increase in the rate of the heart beat from normal to 170 or 200 beats per minute also is possible during exercise. Again, several factors may be involved:

(*a*) Increased temperature. Enough heat is produced by exercising to raise the body temperature a few degrees. This affects the sino-auricular node (just as fever does), and the heart beat rate is increased.

(*b*) Hormones. Both adrenalin, which is produced in increased amounts by the adrenal glands during emergencies, and thyroxin, which is produced by the thyroid gland and quickens body metabolism generally, accelerate the heart beat. When thyroxin is injected into an experimental animal, however, acceleration of the heart does not occur until three or four hours have elapsed—a reaction too slow to be effective in bringing about the rapid adjustment which the heart must make continuously, although it can affect the long-term responses of the heart to the general condition of the body.

(*c*) Nerves. In the normal body, adjustments of the heart beat rate are effected chiefly by two sets of nerves, one of which accelerates it, the other of which slows it down (see Chap. 16).

III. ROUTES OF THE BLOOD AROUND THE BODY

To understand how the circulatory system carries material from one part of the body to another, some knowledge is necessary of how the blood vessels are connected (Fig. 74). In any particular vessel, blood flows in one direction only, of course. The head and brain are supplied with blood by the carotid arteries, and are drained by the jugular veins. In addition, the brain is served by a second pair—the vertebral arteries and veins (not shown on the diagram)—running close to the spinal cord. At the base of the brain are interconnections between the carotid and

vertebral arteries, so that if one of the vessels is cut or occluded, the brain is still adequately supplied with blood.

One exception to the rule that all veins carry blood to the heart is the **hepatic portal system,** which collects blood from the spleen, stomach, pancreas and intestines and conducts it to the liver. There the portal vein breaks up into capillaries which in turn unite to form the hepatic vein, which drains blood from the liver into the inferior vena cava. Because of this arrangement, all blood from the spleen, stomach, intes-

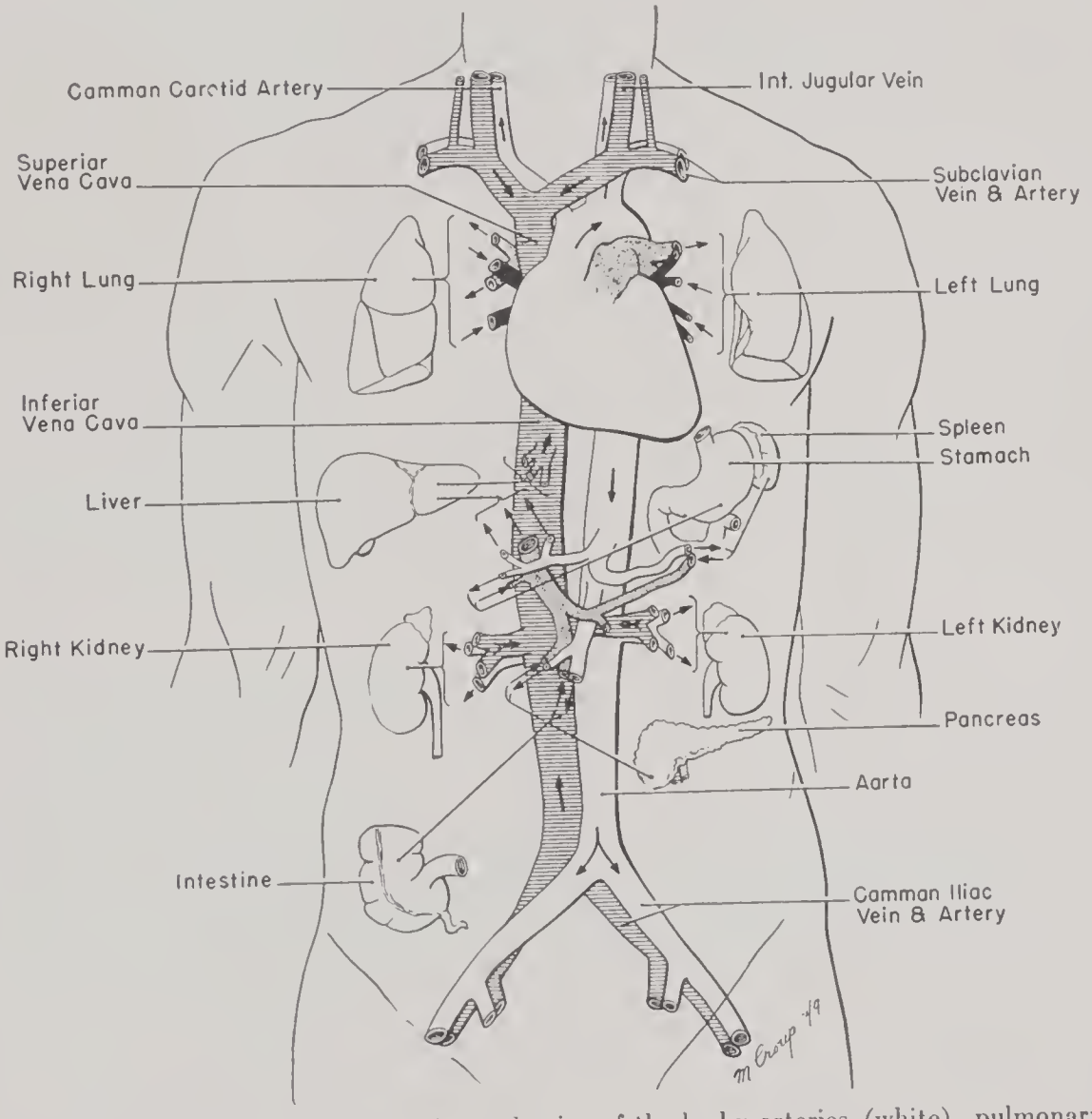


Fig. 74. Diagram of the main arteries and veins of the body; arteries (white), pulmonary artery (stippled), veins (horizontal lines), pulmonary veins (black) and hepatic portal system (dotted).

tines and pancreas must pass through the liver before it reaches the heart. Thus, food absorbed in the intestines is carried directly to the liver for storage.

5. Fetal Circulation and Changes at Birth. A fetus in its mother's womb, or uterus, cannot obtain food or air directly; consequently its stomach and lungs are nonfunctional. It obtains both food and oxygen from the maternal blood by means of blood vessels in the placenta and umbilical cord. There is, however, no direct connection between the blood streams of mother and fetus. The blood of the fetus is manufactured within its own body, chiefly in the spleen and liver. Within the placenta the capillaries of mother and fetus come into close contact,

and substances pass from one to the other by diffusion; oxygen and food substances diffuse from the maternal to the fetal blood vessels, and carbon dioxide and metabolic wastes diffuse from the fetal to the maternal blood vessels. The developing fetus has the remarkable ability to use one set of blood vessels while developing a second set, which must be ready to take over immediately after birth.

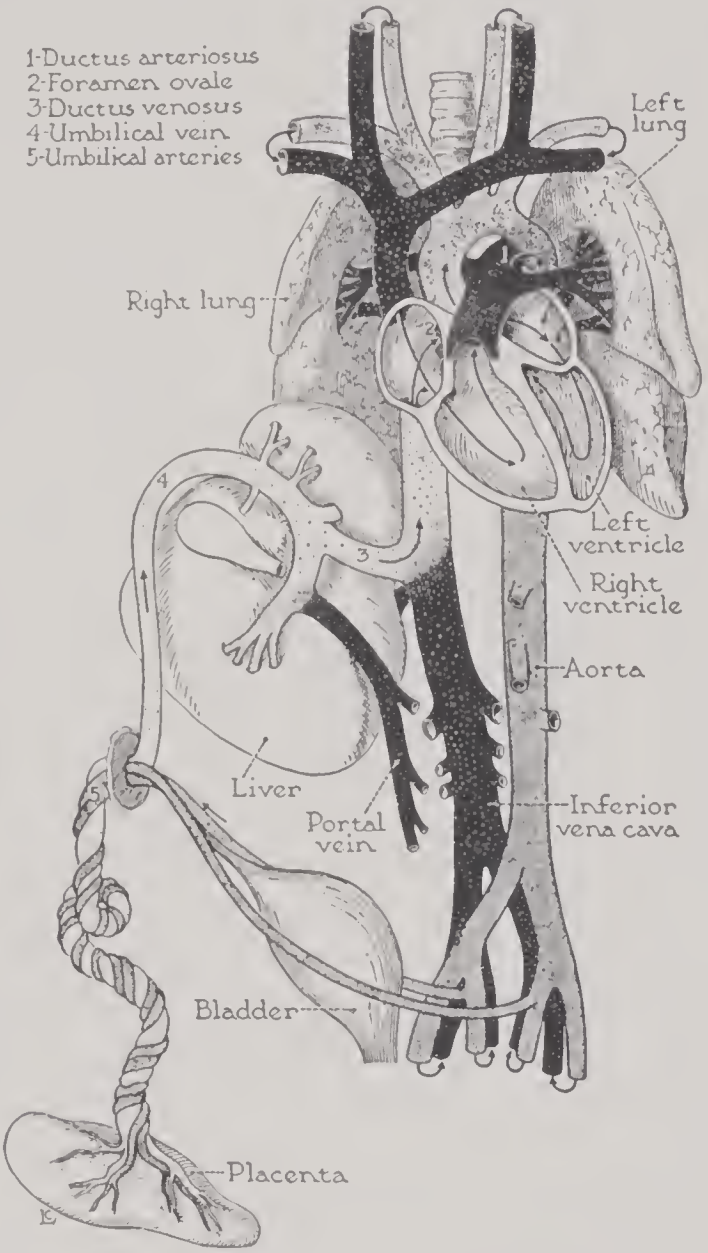


Fig. 75. The human circulatory system before birth. The structures peculiar to the fetal circulatory system are the umbilical arteries and vein to the placenta; the *ductus venosus*, the vein which traverses the liver and connects the umbilical vein with the inferior vena cava; the *ductus arteriosus*, connecting the pulmonary artery and aorta; and the oval window (foramen ovale), connecting the right and left auricles. (Windle, W. F.: Physiology of the Fetus.)

Two **umbilical arteries** grow out of the lower part of the aorta of the fetus and pass to the placenta (Fig. 75). Blood is returned to the child by a single **umbilical vein**, which passes through the liver and empties into the inferior vena cava. The fact that the lungs are small and nonfunctional presents a special problem, for the capillaries in the uninflated lungs can accommodate only a fraction of the blood flowing through the heart; the rest must be passed around the lungs until after birth. This is accomplished by two temporary devices: the **oval window** between

the right and left auricles, and the **arterial duct** connecting the pulmonary artery and the aorta. The opening of the oval window is covered by a flap of tissue which acts as a valve. The blood from the umbilical vein, rich in oxygen and food, is mixed with the blood of the inferior vena cava and passes to the right auricle. Most of this blood then flows through the oval window (pushing the flap of the valve aside, since the blood pressure is higher in the right than in the left auricle) to the left auricle, whence it flows through the left ventricle to the aorta. From the aorta this blood with a high oxygen content passes chiefly to the arteries of the wall of the heart, the head and the forelimbs. Some of it, together with blood entering the right auricle from the superior vena cava, passes into the right ventricle and out the pulmonary artery. Only a fraction of the blood with low oxygen content goes to the lungs; the rest passes across the arterial duct to the aorta. Since the arterial duct joins the aorta beyond the point at which the arteries to the head and arms branch off, this blood passes down the aorta. Only about a third of it goes to the lower part of the trunk and to the legs; the remainder, carried by the umbilical arteries, goes to the placenta, where it receives more oxygen and food. By this arrangement the more rapidly growing head and upper part of the body receive the additional oxygen they need.

At birth, when the infant begins using his lungs, a number of changes must occur quickly. The tying of the umbilical cord deprives the child of that source of oxygen. Carbon dioxide begins to accumulate in the blood stream and stimulates the respiratory center in the brain to bring about the child's first breath. Consequently the lungs and lung capillaries expand, causing more blood to pass through the pulmonary arteries instead of through the arterial duct. This blood, returning to the left auricle, increases the blood pressure in that chamber, and pushes the flap of tissue across the oval window, stopping the flow of blood from the right to the left auricle. This valve eventually grows in place, causing the oval window to be permanently closed. The endothelial lining of the arterial duct grows rapidly to obliterate the cavity of the vessel, and prevent the further passage of blood. Failure of the oval window or the arterial duct to close properly interferes with the normal aeration of the blood; if the condition is extreme, the child may die. If the bypasses close only partially, the hemoglobin is inadequately oxygenated, and a "blue baby" results.* The arterial duct, plus parts of the umbilical arteries and veins, remains within the body and is changed into connective tissue to form ligaments.

6. The Rate of the Flow of Blood. In its course through the body, blood does not flow at a constant speed. The flow is rapid in the arteries (about 500 mm. or 20 inches per second in the larger ones), a little less rapid in the veins (about 150 mm. per second in the larger ones), and slow in the capillaries (less than 1 mm. per second). The differences in the rate of flow depend upon the total cross-sectional area of the vessels. If a fluid passes from one tube into another of larger size, the rate of flow is less in the larger tube. When the blood flows through a series

* The child's skin appears blue because the capillaries are filled with bluish hemoglobin instead of the normal scarlet oxyhemoglobin.

of tubes of different sizes, connected together end-to-end, its velocity is always inversely proportional to the cross-sectional area of whatever tube it happens to be in.

The circulatory system is constructed in such a way that one large artery (the aorta) branches into many, intermediate-sized arteries. These in turn branch into thousands of small arteries (called arterioles), each of which gives rise to many capillaries. Although the branches of the aorta are smaller than the vessel itself, there are so many of them that the total cross-sectional area is greater, and the rate of flow correspondingly less. It has been estimated that the total cross-sectional area of all the capillaries of the body is about 800 times that of the aorta. Therefore, the rate of flow in the capillaries is about $\frac{1}{800}$th as great as in the aorta. At the other end of the capillary network, the capillaries

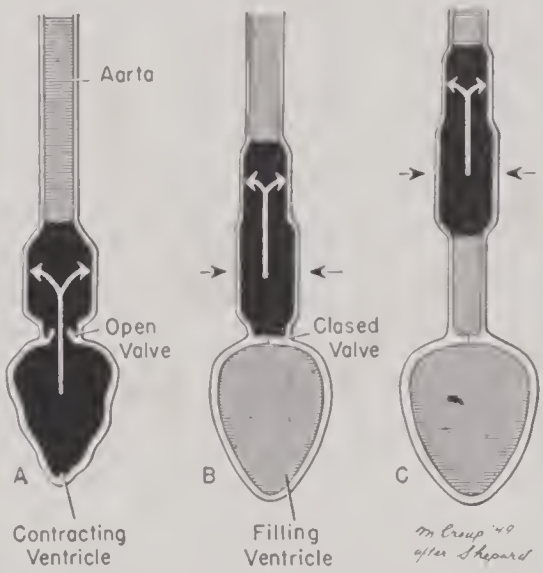


Fig. 76. Diagram of the movement of blood from the ventricle through the elastic artery. For simplicity, only one ventricle and artery are shown, and the amount of stretching of the arterial wall is exggerated. *A*, As the ventricle contracts, blood is forced through the semilunar valves, and the adjacent wall of the aorta is stretched. *B*, As the ventricle relaxes and begins to fill for the next stroke, the semilunar valves close and the expanded part of the aorta contracts, causing the next adjacent part of the aorta to expand. *C*, The pulse wave of expansion and contraction is transmitted to the next section of the aorta.

join to form small veins (venules) which combine to form increasingly larger veins. As this occurs, the total cross-sectional area decreases and the rate of flow increases.

Since the heart pushes blood into the arteries only during ventricular systole, its arterial motion is spasmodic—rapid when the ventricles contract, slow at other times. When the semilunar valves are closed, the blood in that part of the aorta nearest the heart is stationary, but the blood in the arteries farther away from the heart does not stop completely between systoles. In the arterioles the alternation in speeds is less marked; in the capillaries the flow of blood is almost constant, so that transfer of materials can occur continuously. This conversion of the intermittent flow in the arteries to the steady flow in the capillaries is made possible by the elasticity of the arterial wall. The force of the contracting ventricles does two things: it pushes the blood forward, and distends the walls of the arteries (Fig. 76). During diastole the stretched walls contract—as does a stretched rubber band when the stretching

force is removed—thus squeezing the blood along. The blood is prevented from flowing backward by the closure of the semilunar valves. The contraction of the arterial wall next to the heart distends the next section of the aorta or pulmonary artery, which, in turn, contracts and distends the next section, and so on. This alternate stretching and contracting passes along the arterial wall at the rate of 7 to 8 meters (25 feet) per second, and is known as the **pulse.** The blood inside the artery flows at a much slower rate, about 20 inches per second.

Two other factors aid the heart in moving blood through the veins—the movements of the skeletal muscles and the motion of the body in breathing. Most of the veins are surrounded by skeletal muscles, which, when they contract, cause the veins to collapse (Fig. 77). As the muscles relax, the collapsed section again fills with blood, which must come from the direction of the capillaries. This mechanism by which muscle con-

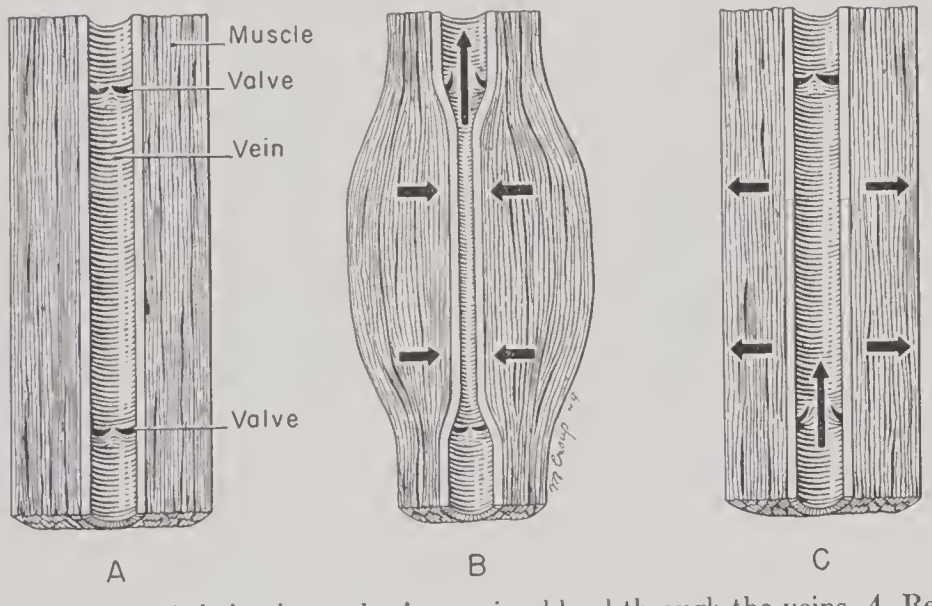


Fig. 77. The action of skeletal muscles in moving blood through the veins. *A,* Resting condition. *B,* Muscles contract and bulge, compressing veins and forcing blood toward heart. The lower valve prevents backflow. *C,* Muscles relax, and the vein expands and fills with blood from below; the upper valve prevents backflow.

tractions "milk" blood along the veins is especially important in returning blood to the heart from the legs against the pull of gravity. If one stands upright quietly for a time, tissue fluid tends to collect in the legs, and swelling (edema) results. In walking, the contractions of the leg muscles force the blood along the veins, and the feet and ankles are less likely to swell. In breathing, the chest muscles and diaphragm contract, increasing the space inside the chest and lowering the pressure within the chest cavity below that outside the body, causing air to flow into the lungs. Since the heart lies within the chest cavity, it too is affected by the breathing movements, and the pressure within the veins in the chest is lowered as one inhales. Blood moves into the chest veins and auricles for the same reason that air moves into the lungs.

These two factors are important in enabling the circulatory system to respond to the increased need for blood during exercise. At that time both the "milking" action of the muscles on the veins and the breathing movements are greatly increased, sending more blood to the auricles.

You will recall that the greater the volume of blood entering the heart, the more the heart muscle is stretched, the more forcibly the heart beats, and the greater the volume of blood ejected per beat. Because of this, the muscular contractions during exertion, which bring about increased requirements for food and oxygen, are partly instrumental in causing the circulatory system to satisfy the increased requirements.

It would be wasteful, however, to have all parts of the body receive an increased supply of blood whenever one part became active. To obviate this, the circulatory system is equipped with a device for regulating the rate at which blood is delivered to any particular part of the body

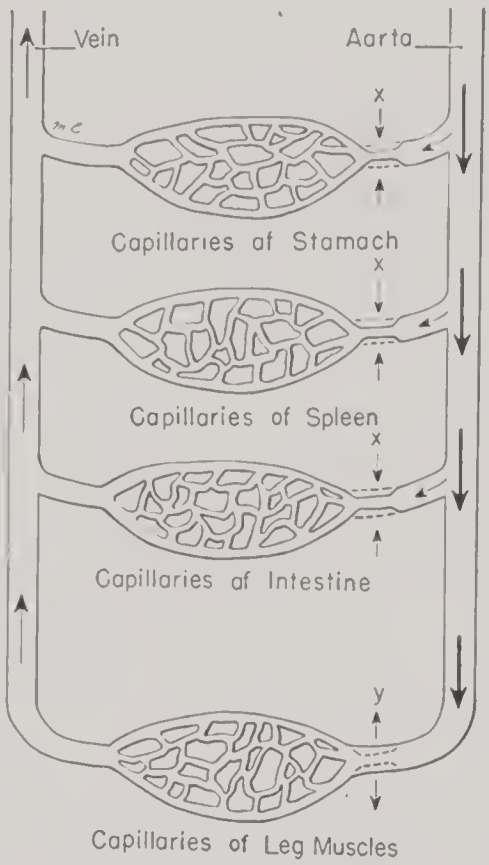


Fig. 78. Diagram of the reactions of the circulatory system during exercise. Contraction of smooth muscles in the walls of the arterioles of the stomach, spleen and intestine (*X*) decreases the diameter of the arterioles and the flow of blood to those organs. Relaxation of smooth muscles in walls of arterioles of leg and other muscles (*Y*) increases the diameter of these vessels and the flow of blood to the skeletal muscles.

(Fig. 78). The walls of the arterioles contain smooth muscle fibers innervated by two sets of nerves. An increase in the number of nerve impulses in one set causes the muscles to contract, decreasing the size of the arterioles and lessening the supply of blood to that organ or part of the body. An increase in the number of nerve impulses in the other set causes the muscles to relax, increasing both the size of the arterioles and the flow of blood to that organ. These muscles usually are partially contracted because of a balance between the two nervous impulses. Because of this nervous mechanism, the arterioles act as valves to regulate the amount of blood each organ in the body receives. The smooth muscles of the walls of the arterioles are affected also by the chemicals—carbon dioxide and epinephrine—which affect the heart output. When a particular organ is metabolizing at a high rate, the greatly increased

amount of carbon dioxide acts directly on the smooth muscles, causing them to relax, and thus increases the delivery of blood to the active tissue. Epinephrine causes a relaxation of the walls of the arterioles serving the skeletal muscles, but a contraction of the walls of the arterioles serving the internal organs—the stomach, intestines and liver—which results in a greatly increased flow of blood to the skeletal muscles. These chemical effects are independent of the nerves, and act equally well on normal arterioles and on those with severed nervous connections.

7. Blood Pressure. The beating of the heart is responsible for the blood pressure in the vessels, causing it to rise with each contraction and to fall with each relaxation of the ventricles. The highest pressure, due to systole of the heart, is called systolic pressure; the lowest, due to diastole, is called diastolic pressure (Fig. 79).

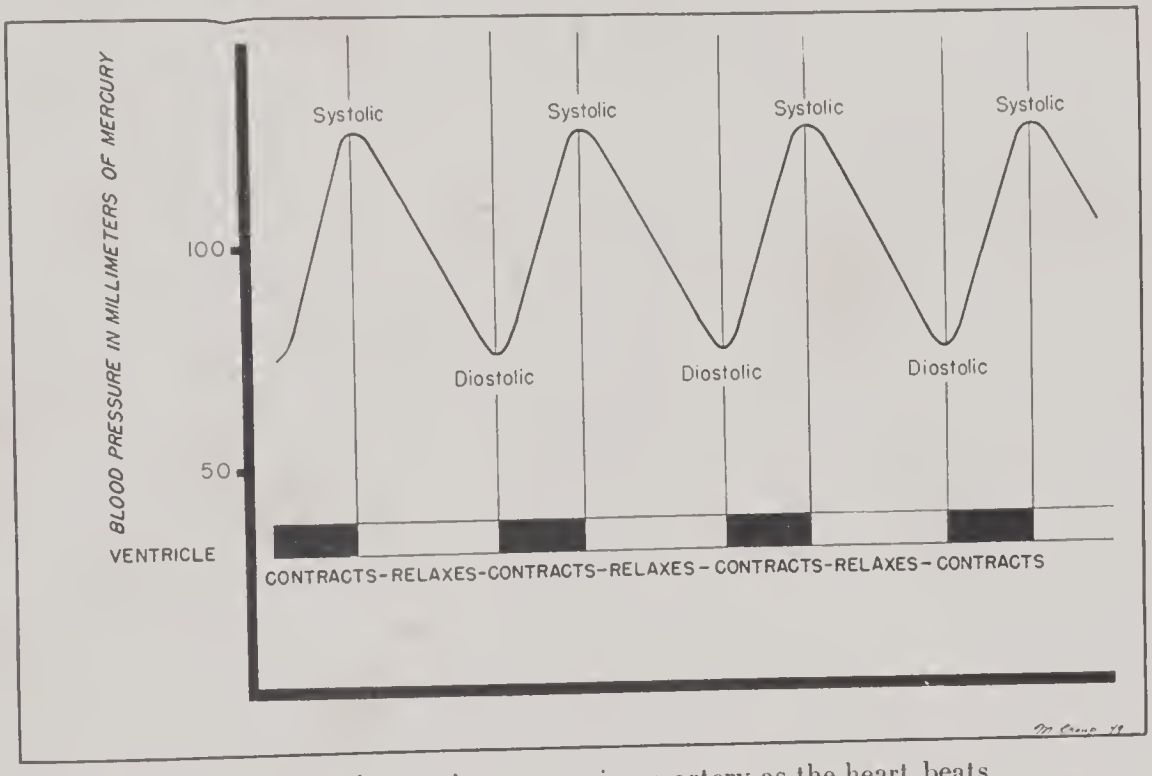


Fig. 79. The changes in pressure in an artery as the heart beats.

The pressure in an artery can be measured directly by inserting a tube into it and measuring the height to which the column of blood rises. An English clergyman, Stephen Hales, made the first such measurement in 1733. He found the blood pressure in the carotid artery of a mare sufficient to cause a column of blood to rise 9½ feet in a glass tube.

Because it is not practical to puncture an artery in a human being each time the blood pressure is taken, a device known as a **sphygmomanometer** is used. This consists of a cuff, tied around the arm, containing a rubber bag, to which is attached a rubber bulb and a device for measuring pressure (Fig. 80). The pressure of the blood pushing against the sides of the arteries (Fig. 81, *A*) is measured by determining how much pressure in the rubber bag causes the artery to collapse. Systolic pressure corresponds to the pressure in the bag which is just enough to obliterate the wrist pulse (Fig. 81, *B*). To measure diastolic pressure, a stethoscope is placed over the arm artery below the cuff so that the noise produced by the pulsing of the blood can be heard. When the

pressure in the cuff is just below systolic pressure (Fig. 81, *C*), a small amount of blood passes the constriction each time the pressure rises at systole. This blood strikes the stationary blood beyond the cuff, producing vibrations audible in the stethoscope. As the pressure in the cuff is gradually lowered, more and more blood passes at each systole, producing an increasingly loud noise (Fig. 81, *D*). When the pressure in the cuff is just above diastolic pressure, the noises are loudest, and as the cuff pressure drops below it, the blood flows continuously and no noises are audible (Fig. 81, *E*).

In man and many mammals, systolic pressure is about 120 mm. of mercury (i.e., equal to the pressure of a column of mercury 120 mm.

Fig. 80. Determining the blood pressure by means of a sphygmomanometer. Using a stethoscope, the physician can detect the increase and decrease in noise of the blood flowing through the artery beyond the rubber cuff, as the pressure in the cuff is raised and lowered. (Crandall, L. A.: Introduction to Human Physiology.)

high), and diastolic pressure about 75 mm. The difference between systolic and diastolic pressures—that is, the change in pressure that occurs each time the heart beats—is called the **pulse pressure.** The arterial pressure, usually measured in the artery of the left arm just above the elbow, is recorded as a fraction, with the systolic pressure as the numerator and the diastolic pressure as the denominator: 120/75. Therefore, when a physician tells you that your blood pressure is 120, he is referring to the pressure in a particular artery in the arm, and does not mean that the blood all over your body is under the same pressure. The blood pressure decreases along the circulatory system from the aorta to the veins, being greatest in the aorta (as high as 140) and lowest in the veins near the auricles, where it approaches or even falls below zero, i.e., atmospheric pressure. (Fig. 82). The decrease in pressure is

caused by the friction of the blood rubbing against the walls of the blood vessels, and is especially marked in the arterioles and capillaries, because those vessels are small and friction is greatest. The gradual decrease in pressure is necessary to keep the blood flowing; if the pressure were the same throughout the circulatory system, the blood would not move.

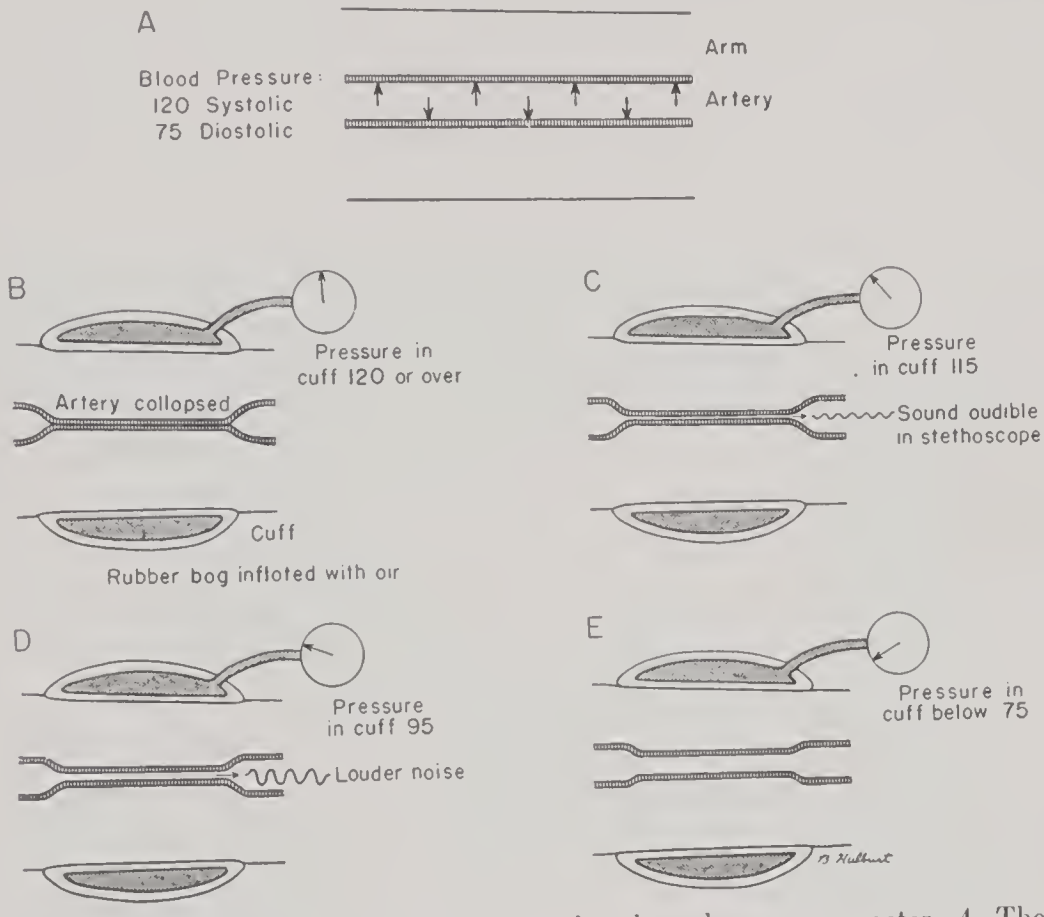


Fig. 81. The measurement of blood pressure by the sphygmomanometer. *A*, The blood pushes against the arterial walls with a pressure (systolic) of 120 mm. of mercury when the heart contracts, and a pressure (diastolic) of 75 mm. of mercury when the heart is relaxed. *B*, When the air pressure in the rubber cuff exceeds 120 mm. of mercury, the arm is constricted, the artery is collapsed, and no blood passes. *C*, With the pressure in the cuff just below 120, the artery is collapsed except for a small period during systole, when a small amount of blood squirts through, producing a sound audible in the stethoscope. *D*, With the pressure in the cuff at 95, the artery is open for a longer time during systole, a greater amount of blood passes through, and a louder noise is produced. *E*, When the pressure in the cuff drops below 75, the artery is open continuously, blood passes through continuously, and no noise is heard. Thus systolic pressure is that at which a noise is first heard, as the pressure in the cuffs is lowered, and diastolic pressure is that at which the noises cease.

The high pressure in the arteries is necessary to force blood through the capillaries, where resistance due to friction is great, as well as to force blood back to the heart through the veins. This pressure has to be sufficiently strong to force blood up to the brain against the pull of gravity, and to return blood from the legs against the same force. High pressure is also necessary to ensure rapid adjustments of the blood flow to certain organs as their needs change; as the arterioles of an organ dilate, high pressure is needed to cause an immediate inrush of blood.

8. The Role of Blood Pressure in the Exchange of Materials in the Capillaries. As the blood passes through the capillaries, a decrease in its pressure occurs, from about 40 (mm. of mercury) on the side of the

capillaries next to the arterioles, to about 10 on the side next to the venules. This enables water and substances dissolved in the blood to filter out of the capillaries into the tissue fluid. Remember that blood plasma contains proteins which exert an osmotic pressure, tending to

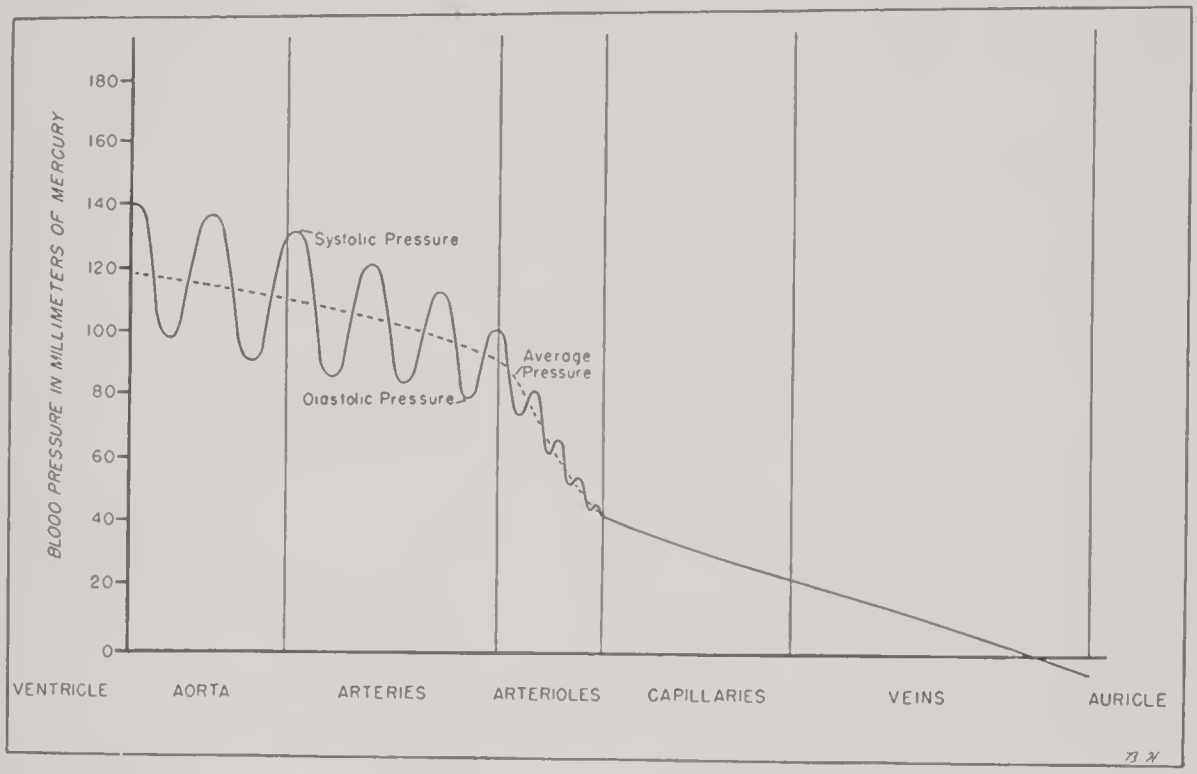


Fig. 82. Diagram showing the blood pressure in the different types of blood vessels of the body. The systolic and diastolic variations in arterial pressures are shown. Note that the venous pressure drops below zero (below atmospheric pressure) near the heart.

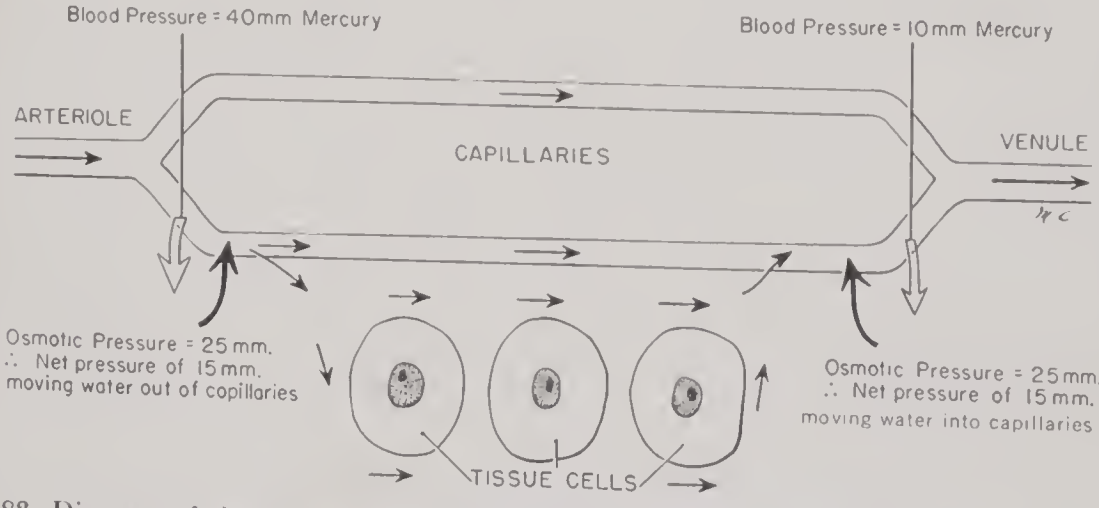


Fig. 83. Diagram of the forces responsible for the exchange of materials between capillaries and tissue fluid.

cause water to move into the capillaries. The osmotic pressure is the same at both ends of the capillaries, exerting the same pressure as about 25 mm. of mercury. Thus in the capillaries near the arterioles there is a net pressure of some 15 mm. (40 minus 25) which pushes water out of the capillaries (Fig. 83). At the other end, near the venules, there is a net pressure of about 15 mm. (25 minus 10) pulling water back into the capillaries. Under normal conditions the blood volume remains constant because equal quantities of water pass in and out. This device is impor-

tant in maintaining a constant stream of fresh tissue fluid and its dissolved nutrients past each cell of the body.

It is important, too, in replenishing the liquid of the blood after hemorrhage. In such circumstances the decrease in blood volume causes a decrease in blood pressure and hence in filtration pressure. But the amount of proteins per cubic centimeter of blood remains the same, so that osmotic pressure is not diminished. This results in a lowered net pressure to move water out of the capillaries at the arterioles, and an increased net pressure to move it into the capillaries at the venule end, thereby increasing the blood volume at the expense of the tissue fluid. This is a temporary measure to prevent heart failure from a lack of blood to be pumped, and true recovery does not occur until later when new blood is manufactured.

"Shock" is a condition frequently present after surgical operations, burns, accidents or severe fright. It is characterized by an increased permeability of the walls of the capillaries, which, by allowing the plasma proteins to escape, lowers the osmotic pressure that normally returns fluids to the capillaries. As a result, fluids escape from the capillaries to the tissues, the blood volume decreases, and, in severe cases, death results. The danger from the shock accompanying severe wounds has been greatly lessened by the use of repeated plasma transfusions which replace the lost plasma proteins and prevent the loss of fluids from the capillaries.

IV. HEART AND VESSEL DISORDERS

The heart is subject to several conditions which interfere with its ability to pump. Severe muscular exercise by a person in poor physical condition may strain and damage the heart muscle and reduce its ability to contract. Or the blood vessels leading to the heart muscle may become clogged by a blood clot or some other object which cuts off the supply of food and oxygen, resulting in a heart "attack." If the area of the heart served by the plugged vessel is not too large, the attack will not be fatal; but if a large area is affected, death results within a few minutes. Certain diseases, such as diphtheria, produce poisons which reach the heart via the blood stream and injure the heart muscle. An excess of thyroid hormone causes the auricles to beat in an uncoordinated way so that efficiency is impaired. Sometimes the heart valves, damaged by disease organisms such as those of syphilis or rheumatic fever, are unable to close properly, and blood leaks back after the heart contracts. To compensate for this, the heart often enlarges to increase its pumping ability. Rheumatic fever, which is especially prevalent among young people, is dangerous, not because of the infection of the joints—its primary effect—but because of the secondary effect, heart disease.

As one grows older, the walls of the arteries, tending to lose their elasticity, become harder and thicker, reducing the size of the cavity. Less blood then passes to the organs, which are unable to function properly. Usually, an increase in blood pressure accompanies the hardening of the arteries, for as they lose their elasticity and are unable to expand and contract each time the heart beats, the latter must pump harder to force the blood along. High blood pressure may be caused by

other disorders—kidney disease, for example—and is dangerous because, if excessive, it may burst a blood vessel. Usually, only a small vessel bursts, and the loss of blood is not important. But bleeding in a soft structure such as the brain may damage the cells, resulting in paralysis of the muscles served by them, and sometimes death ensues. High blood pressure may bring about heart failure by forcing it to enlarge in order to drive the blood against the increased resistance of the hardened arteries.

The veins sometimes swell, causing large pools to form within the vessels (a condition called varicose veins). Varicose veins occur almost always in the legs, and are most frequently the affliction of people who have to stand a great deal. Standing still increases the pressure in the leg veins by depriving them of the "milking" action of the leg muscles, which ordinarily helps to return the blood properly. But the ultimate causes of the condition, and the reason why it is more prevalent among women than among men, are obscure.

V. THE LYMPH SYSTEM

Besides the blood circulatory system, the body is equipped with a similar, independent group of vessels constituting the **lymph system.** These vessels carry the clear, colorless fluid, lymph, which, like tissue fluid, comes from the blood by diffusing through the walls of the capillaries, and so resembles it closely. But it contains much less protein than does blood (because the protein molecules are large and diffuse slowly) and no red cells. It does contain white cells, some of which enter the lymph capillaries from the tissue fluid, others of which are manufactured in the lymph nodes. In other respects lymph is similar to blood.

The lymph system differs from the blood system in that its vessels serve only to *return* fluid to the heart. There are no arteries in this system, only capillaries and veins distributed all over the body. The capillaries are extremely tiny vessels, with walls only one cell thick, which resemble blood capillaries, except that they are closed at one end (Fig. 84). Lymph diffuses into these capillaries from the surrounding tissue fluid. At the other end the capillaries connect with lymph veins, which resemble blood veins in having valves and thin walls. These in turn empty into successively larger veins, the biggest of which drains into the left shoulder vein of the blood system. It is important to remember that fluids reach the cells of the body by one route only: the arteries, arterioles and capillaries of the blood circulatory system. But there are two possible return routes: the blood capillaries and veins, and the lymph capillaries and veins.

At the points where the lymph vessels join are aggregations of cells known as **lymph nodes,** analogous to the pillboxes in a military line of defense. These manufacture lymphocytes and filter out dust particles and bacteria to prevent their entering the blood stream. The channels by which the lymph passes through the nodes are so minute and tortuous that its flow is sluggish, and invading bacteria can be caught and phagocytized by the white cells. Some bacteria may get past the first lymph node and be caught by the second or third; in a massive infec-

tion the bacteria may penetrate all the lymph nodes and invade the blood stream. But even in such cases the lymph nodes are valuable in delaying the spread of the infection, thus giving the body time to accumulate white cells to fight it. The presence of infectious organisms causes the lymph nodes to become swollen and tender—thus the lymph nodes of the neck become noticeably swollen in cases of sore throat. In the lymph systems of city dwellers and heavy smokers the nodes near the lungs become filled with particles of dust and soot and are a dark gray or black. These particles may eventually interfere with the functioning of the lymph nodes, and lower resistance to lung infections, such as tuberculosis.

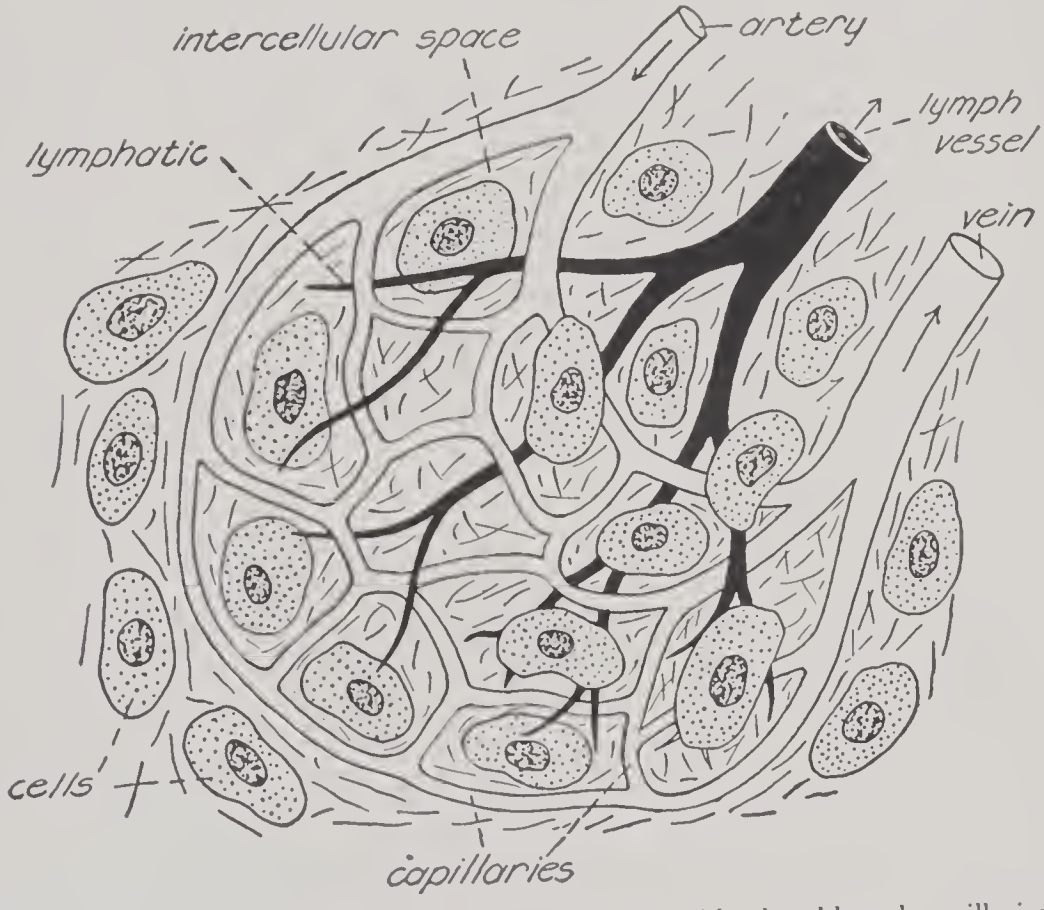


Fig. 84. Diagram of the relation between tissue cells and blood and lymph capillaries. Note that blood capillaries (white) are connected at both ends, whereas lymph capillaries (black) are "dead end streets." (Curtis and Guthrie: General Zoology, John Wiley and Sons, Inc.)

9. The Flow of Lymph. Unlike many of the lower animals,* man has no organ to move the lymph along. It is made to flow simply by the mechanisms which aid the heart in causing blood to flow in the veins—the movements of the adjacent skeletal muscles, which compress the lymph vessels (the valves prevent its backflow), and the breathing movements of the chest. The flow of lymph from the intestine is aided by the movements of the villi, the finger-like projections from the wall of the intestine into its cavity, which contract and relax spasmodically. The rate of the flow of lymph is much slower than that of blood.

* The frog, for example, has four lymph "hearts" which pulsate and squeeze the lymph forward. These hearts are simply thicker-walled, muscular parts of the lymph vessels, and have no chambers or special valves.

10. Functions of the Lymph System. The lymph system performs four functions. First, it assists in returning tissue fluids to the blood circulatory system. Since, normally, the walls of the blood capillaries are slightly permeable to the proteins of the plasma, there is a slow, constant leakage of these proteins into the tissue fluid. Without the lymph system the concentration of protein in the tissue fluid would eventually equal the concentration in the blood capillaries. This would interfere with the mechanism that draws tissue fluid into the blood capillaries at their venous end, and so result in swelling (edema). The tremendous swellings of elephantiasis are caused by the blocking of the lymph channels by a parasitic worm (called a filaria) which is injected into the body by the bite of a mosquito.

We have already noted two other functions of the lymph system—the manufacture of lymphocytes, and the filtering of dust and bacteria. A fourth function, the absorption of fats, is accomplished by the lymph vessels which drain the intestines. The products resulting from the digestion of carbohydrates and proteins are absorved directly into the blood capillaries, but most digested fats are absorbed into the lymph capillaries in the walls of the intestine and carried by the lymph vessels to the left shoulder vein, whence they are emptied into the blood stream. Why fats should be absorbed in this way is unknown.

From the foregoing discussion you can understand why the lymph system has an important relation to the spread of cancer throughout the body. Cancer is a condition in which certain cells become overactive in growth and cell division, increasing at the expense of the surrounding cells. The stimulus for this may be certain chemicals; X-rays or other rays; the presence of unusual parasites within the cells; and probably other factors. Whatever the cause, the cells proliferate and cause a swelling. They may then break off from the original mass, find their way into a lymph vessel and be carried by it to other parts of the body. If treatment is begun in time, cancer is curable by surgery or radiation, because the lymph nodes prevent the cells from spreading rapidly. In cutting out a cancerous growth, the surgeon must be careful to remove the adjacent lymph nodes, which may contain cancerous cells capable of instigating a recurrence of the condition.

VI. CIRCULATION IN OTHER ORGANISMS

All organisms have the same problem of transporting substances from one part of the body to another. The human heart, with its remarkable automatic devices for keeping the blood flowing and for adapting to changing conditions, is the result of a long evolutionary process. In the simplest plants and animals—the microscopic ones whose bodies are made of a single cell—the transportation problem is correspondingly simple. Materials get from one part of the cell to another by diffusion. In some of these organisms the cytoplasm of the cell undergoes streaming movements which aid in the distribution of foods and the collection and removal of wastes.

11. Circulation in Animals. The single-celled animals, protozoa, have no special system for bringing about the circulation of substances; foods.

wastes and gases simply diffuse through the cytoplasm and eventually reach all parts of the cell. In most protozoa this process is aided by movements of the cytoplasm. As an ameba moves along, the cytoplasm streams from the rear to the front of the body, distributing substances throughout the cell (Fig. 85, *A*). In other types of protozoa, such as the *Paramecium,* which has a firm, outer shell and does not change shape as it moves, substances are distributed by a rhythmic, circular movement of the cytoplasm in the direction indicated by the arrows in Figure 85, *B*. Food is taken in through a "mouth" and gullet on one side of the animal, and food vacuoles form at the base of this gullet to break off and move through the cell as they digest and give off food. Gases and waste products of metabolism are moved similarly.

The coelenterates—the group of many-celled animals, including hydras, corals, jellyfishes and sea anemones—have a simple body plan. The body wall consists of two layers of cells surrounding a central cavity

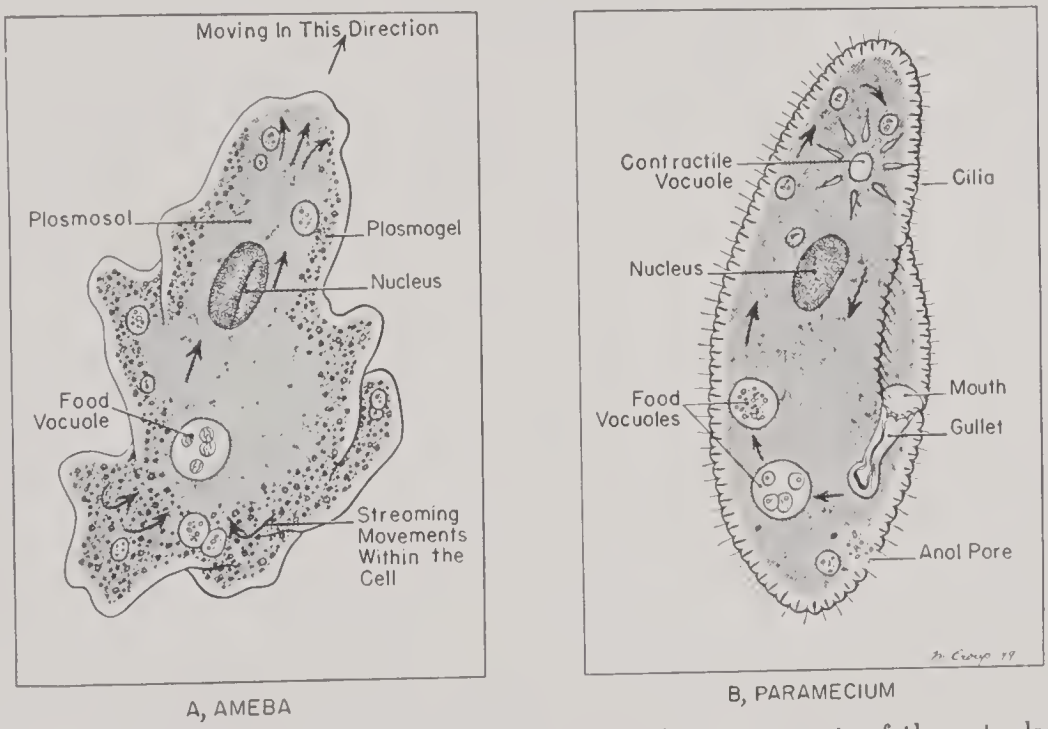


Fig. 85. Circulation in protozoa by means of streaming movements of the cytoplasm.

(Fig. 103), which serves both as a digestive and circulatory organ. In the center of the bases of the tentacles a mouth opens into this central cavity. When the tentacles have captured their prey they stuff it through the mouth into the cavity, where digestion occurs. The digested food substances then pass to the cells lining the cavity and through them, by diffusion, to the outer layer. The movement of the animal's body, as it alternately stretches and contracts, stirs up the contents of the central cavity and aids circulation.

The flatworm planaria (Fig. 103) resembles the hydra in having a single, central cavity connected to the outside by a single mouth opening. But besides the inner and outer layers of cells found in hydra, the planaria has a third layer of cells, loosely packed between the other two. The spaces between these cells are filled with a tissue fluid somewhat similar to the tissue fluid of human beings. Food enters through the mouth, is digested in the central cavity, diffuses through the inner layer

of cells and passes through the tissue fluid to the other cells. As in the coelenterates, circulation is aided by the contraction of the muscles in the body wall which agitate the fluid in the central cavity and the tissue fluid.

In the earthworm and similar forms there is a definite circulatory system, consisting of plasma, blood cells and blood vessels, although the latter are not specialized as arteries, veins and capillaries. There are two main blood vessels, one on the ventral side, in which blood flows posteriorly (Fig. 53), and one on the dorsal side, in which it flows anteriorly. Connecting these in each part of the body are small tubes which serve the intestine, skin and other organs. In the anterior part of the worm are five pairs of "hearts" or pulsating tubes which conduct blood from the dorsal to the ventral vessel to complete the circuit. The contractions of the muscles of the body wall aid the hearts in circulating the blood.

The larger and more complex invertebrates, such as clams, squids, crabs and insects, all have a circulatory system consisting of a heart, blood vessels, plasma and blood cells. The heart is different from a vertebrate heart, consisting in most forms of a single muscular sac. The blood vessels from the heart open into large spaces, enabling the blood to bathe the body cells. From these spaces, blood is collected by other vessels and returned to the heart. The details are different in various animals; but in all, the circulatory system performs the functions of supplying the cells of the body with oxygen and nutrients, and of removing metabolic wastes.

The circulatory systems of all vertebrates are fundamentally the same, from fish and frogs through lizards to birds and man. All have hearts and an aorta, as well as arteries, capillaries and veins, organized on a similar basic plan. Because of this similarity, students can learn much about the human circulatory system from the dissection of a dogfish or frog.

In the evolution of the higher vertebrates, such as man, from the lower, fishlike forms, the principal change in the circulatory system occurred in the heart, and is correlated with the change in the respiratory mechanism from gills to lungs. The fish heart consists of four chambers in a row: sinus venosus, auricle, ventricle, and conus (Fig. 86, *A*). Blood from the veins drains into the sinus venosus, while blood from the conus is pumped through the ventral aorta to the gills, where it takes up oxygen. It then goes to the dorsal aorta and is distributed to all parts of the body. Blood passes through the fish heart only once each time it makes a circuit through the body.

In the particular group of fish from which the land vertebrates evolved, a number of changes occurred in the heart and blood vessels which are visible in present-day frogs (Fig. 86, *B*). A partition developed down the middle of the auricle, dividing it into right and left halves. The sinus venosus shifted its connection so that it emptied only into the right auricle. A vein from the lungs emptied into the left auricle, while pulmonary arteries to the lungs grew out of the vessels which originally served the most posterior pair of gills. Thus, in the frog, blood should pass from the veins to the sinus venosus, to the right auricle, to the ventricle to the aorta, the pulmonary arteries, the lungs, the pul-

monary veins, the left auricle, the ventricle, the aorta, and then to the cells of the body. Of course, there is some mixing of aerated and nonaerated blood in the ventricle, and some blood from the sinus venosus may get into the aorta instead of the pulmonary artery, while some from the left auricle may be pumped into the pulmonary artery. There is less mixing than one might suppose, however. Blood from the right auricle

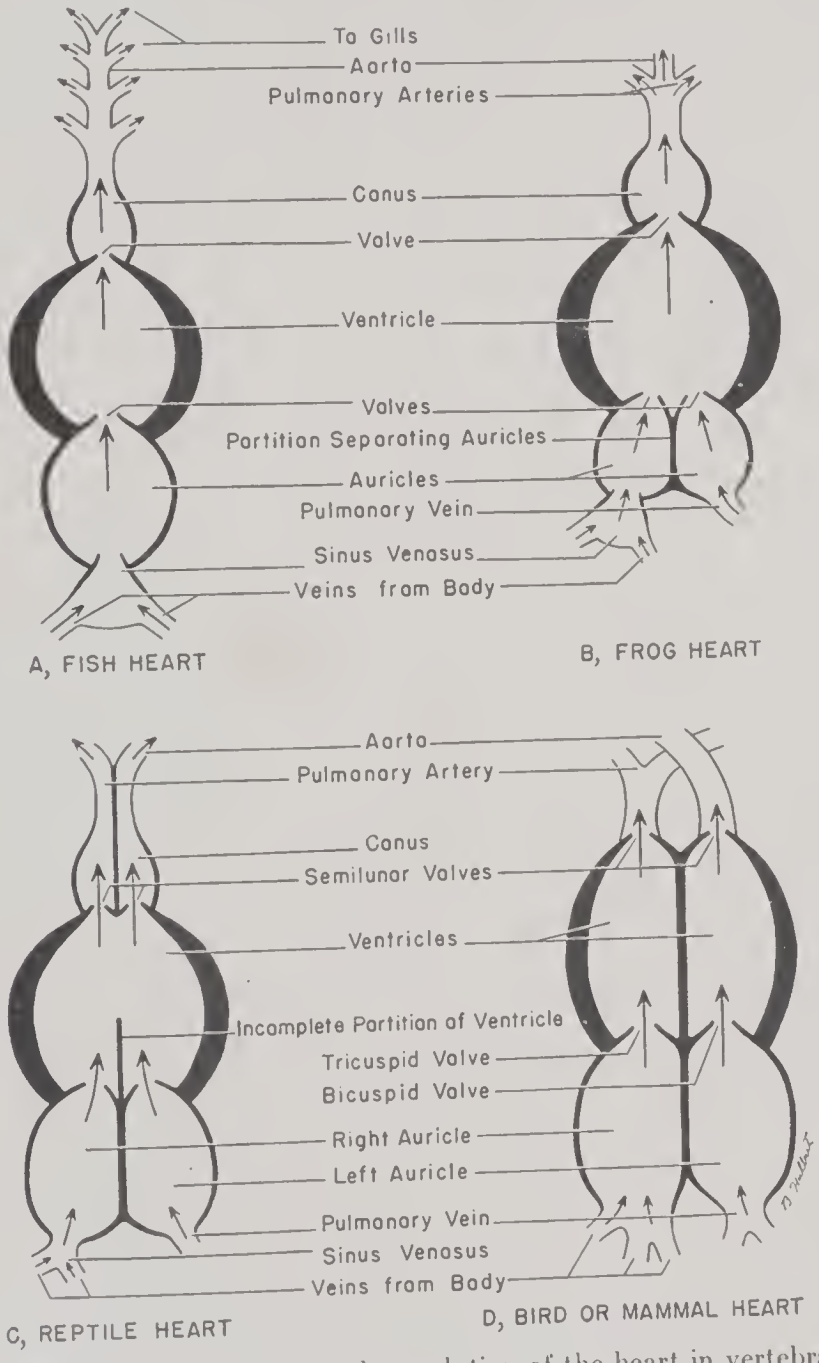


Fig. 86. Diagrams illustrating the evolution of the heart in vertebrates.

enters the ventricle ahead of that from the left auricle, and so lies nearer the exit. As the ventricle contracts, nonaerated blood from the right auricle leaves first and enters the arteries branching off from the aorta —the pulmonary arteries to the lungs. The aerated blood from the left auricle leaves the ventricle toward the end of the contraction, is unable to enter the pulmonary arteries because they are full of other blood, and so passes via the aorta to the body cells. Because aerated and nonaerated blood may mix in the ventricle, blood may pass through the

heart once, twice or even more times for each circuit it makes through the body.

In the evolution of reptiles from their ancestral amphibians, one partition developed down the center of the ventricle, and one down the conus (Fig. 86, *C*). Since the ventricular partition is incomplete in all the reptiles except alligators and crocodiles, there is still some mixing of aerated and nonaerated blood, although less than in the frog. The sinus venosus is small, foreshadowing its disappearance in the mammalian heart.

The hearts of birds and mammals (Fig. 86, *D*) show the complete separation of right and left sides. The interventricular partition also is complete, precluding any mixture of blood from the right and left hearts. The conus has split and become the base of the aorta and pulmonary artery. The sinus venosus has disappeared as a separate chamber, although a vestige remains as the sino-auricular node. The absolute separation of right and left hearts forces the blood to pass through the heart twice each time it makes a tour of the body. As a result, the blood in the aorta of birds and mammals contains more oxygen than that in the aorta of the lower vertebrates. Hence the tissues of the body receive more oxygen, a higher metabolic rate can be maintained, and the warm-blooded condition is possible. Fish, frogs and reptiles are cold-blooded primarily because their blood lacks sufficient oxygen to permit the rapid burning of fuel necessary to maintain a high body temperature in cold surroundings.

12. Circulation in Plants. The circulatory systems of higher plants are simpler than those of higher animals, and are constructed on an entirely different plan. Plants have no heart or arteries, no veins or capillaries. Transportation is accomplished in these forms by the xylem and phloem systems, and a few plants have an additional latex system to assist in circulation (see Chap. 6). Many plant cells are near enough to the surface to obtain their oxygen and carbon dioxide directly from the atmosphere. The rest receive their oxygen from the air spaces, or canals, that penetrate the deeper parts of the plant, and the xylem and phloem tubes have little or nothing to do with the transportation of gases. There is a further division of labor in that the xylem tubes are chiefly concerned with transporting water from the roots up the stem to the leaves, while the phloem tubes transport food which has been manufactured in the leaves, down the stems for storage and use in the stems and roots. The connections of the phloem and xylem vessels are fundamentally different from those in arteries and veins, where a large tube branches successively into smaller and smaller tubes. All xylem and phloem tubes are small, and occur in bunches called vascular bundles. In the lower part of the stem there are many vessels per bundle; in the upper part there are fewer per bundle, the others having entered the branches of the stem.

QUESTIONS

1. How do food and oxygen actually get into the cells of the body?
2. What is the route of the blood through the heart? What part do the semilunar valves play in its passage?
3. What regulates the heart beat?
4. What actually happens when the heart "beats?"

5. How does the developing embryo obtain food and oxygen?
6. Where in the body does the blood flow most slowly? Why?
7. What is meant by systolic and diastolic pressure?
8. What physiological changes occur during "shock"?
9. What is lymph? How does it differ from blood?
10. What are the two ways (in man) by which fluids may return to the heart?
11. Compare the manner in which food and oxygen are carried about the body in an amoeba, a hydra, a planaria, a crab and a frog.
12. What is the principle difference between the circulatory system of a fish and that of a man?
13. Why is circulation in plants much simpler than in animals?
14. Trace the path of a red blood cell from a vein in the leg to the kidney.
15. Trace the path of a molecule of sugar from the capillaries of the intestine to a brain cell where it is burned, and then trace the path of the carbon dioxide formed by this combustion, until it is finally excreted by the lungs.

SUPPLEMENTARY READINGS

Best, C. H., and Taylor, N. B.: *The Living Body*. New York, Henry Holt & Company, Inc., 1944.
A clear, understandable presentation of human physiology.

Carlson, A. J., and Johnson, V.: *The Machinery of the Body*. 3rd ed. Chicago, University of Chicago Press, 1948.
A well-written and illustrated discussion, on a fairly simple level, of human physiology.

Fulton, J. F.: *Howell's Physiology*. 16th ed. Philadelphia, W. B. Saunders Company, 1949.
One of the standard, detailed, advanced texts of physiology.

Gerard, R. W.: *The Body Functions*. New York, John Wiley & Sons, Inc., 1941.
An interesting account of circulation, digestion and excretion in man.

CHAPTER 10

THE RESPIRATORY SYSTEM

FROM the most highly organized and complex animals, such as cats or chimpanzees, to the simplest, one-celled animals and plants, such as paramecia or algae, all the amazing functions peculiar to living matter—the ability to think, to work, to grow, to reproduce, to move even so much as a fraction of an inch—depend upon one of the components of the air: oxygen. This is so because the energy to perform these acts comes to the organism locked up in food, and must be "released" or changed from the potential form into the usable, kinetic form. Oxygen is the element which brings this change about. Seventy-nine per cent of air is nitrogen, but this gas is completely inert and plays no part in the chemical reaction of the cells.

Ultimately, all energy in the world comes from the sun as radiant energy, and we have seen how, by using this, the green pigment of plants, chlorophyll, catalyzes the manufacture of sugar (glucose) from carbon dioxide and water. The glucose may then be changed into various substances—proteins, fats and other carbohydrates—which animals use for food. Such foods are finally changed back into glucose, and are then ready to be acted upon by oxygen.

When the oxygen from the environment comes in contact with this glucose, a basic chemical reaction occurs: the oxygen molecules combine with the glucose molecules to form two different substances, water and carbon dioxide. In so doing, the energy which previously was used to hold the glucose molecules together is freed (since the glucose as such passes out of existence) and is used by the body to do work.*

1. Direct Respiration. Animal cells, then, need a constant supply of oxygen to carry on metabolism. The cells of the body die quickly if deprived of this element; certain brain cells are damaged beyond repair if their supply is cut off for only three or four minutes. But it is just as necessary that the carbon dioxide produced in this series of changes be removed. The process whereby animal and plant cells take in oxygen and give off carbon dioxide is called **respiration.** It is a fairly simple process in a small, aquatic animal such as a paramecium or a hydra: dissolved oxygen from the surrounding pond water diffuses into the cells, the carbon dioxide diffuses out, and no special respiratory system is needed. On this level it is called **direct respiration,** because the cells of the organism exchange oxygen and carbon dioxide directly with the surrounding environment.

* The over-all reaction, written in chemical shorthand, is as follows: $C_6H_{12}O_6+6O_2 \longrightarrow 6CO_2+6H_2O+$energy. However, cells would be unable to utilize the large amount of energy set free if a molecule of glucose were oxidized all at once; so a complicated series of enzyme-controlled reactions breaks down the glucose molecule into a long series of intermediate substances and releases the energy in small batches, in a form the cell can use.

2. Indirect Respiration. As animals evolved into higher, more complex forms, it became impossible for each cell of their bodies to exchange gases directly with the external environment. Some form of **indirect respiration** involving a structure of the body specialized for respiration was necessary. This specialized structure had to be thin-walled (the membrane of the wall must be semipermeable), so that diffusion could occur easily; it had to be kept moist, so that oxygen and carbon dioxide had water to be dissolved in; and it needed a good blood supply. For indirect respiration, fishes, crabs, lobsters and many other animals developed gills; the higher vertebrates, reptiles, birds and mammals developed lungs; the earthworm uses its moist skin; and insects use tracheal tubes, canals running all through the body, connected by pores with the external environment.

In indirect respiration two phases, an external and an internal one, are involved in the exchange of gases between the body cells and the environment. **External respiration** consists in the exchange of gases by diffusion between the external environment and the blood stream, by

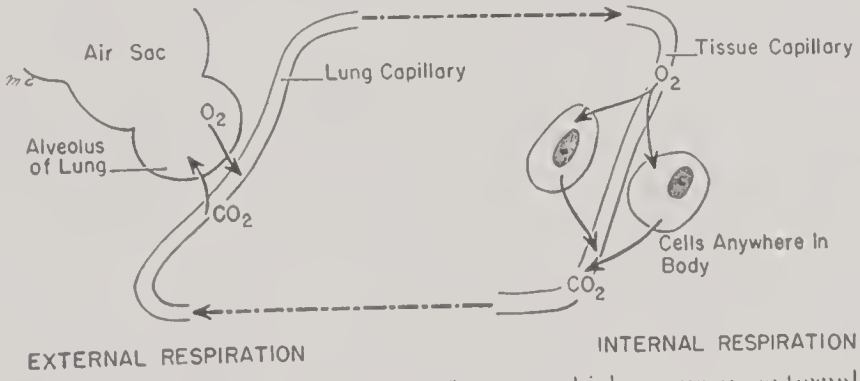


Fig. 87. Diagram illustrating the exchanges of gases which occur in external and internal respiration.

means of the specialized respiratory organ—for example, the lung in mammals. **Internal respiration** consists in the exchange of gases between the blood stream and the cells of the body (Fig. 87). Between these phases the gases are transported by the circulatory system.

3. Structure of the Human Respiratory System. The respiratory system in man and other air-breathing vertebrates consists of the lungs and the tubes by which air reaches them. The anatomy of this system may be understood by tracing the path of the oxygen molecules entering the body (Fig. 88). Air enters through the **external nares,** or nostrils, which open into the **nasal chamber,** a large cavity dorsal to the mouth cavity and ventral to the brain. This cavity contains the sense organ of smell, and is lined with mucus-secreting epithelium, which cleans and warms the air as it passes through. (When the capillaries in this chamber dilate excessively, causing an oversecretion of mucus, the nose becomes "stopped up" and we have the symptoms of a cold.) The air continues on via the **internal nares,** which connect with the pharynx.

In the **pharynx** the paths of the digestive and respiratory systems cross. Food passes from the pharynx to the stomach by way of the esophagus, and air leaves by way of the larynx and trachea. To prevent food from passing into the larynx and trachea and injuring the delicate

membranes lining them, a flap of tissue, the epiglottis, folds over the opening of the larynx whenever food is swallowed. Fortunately, this is done automatically so that we do not have to remember to close the epiglottis each time we swallow; but sometimes the automatic mechanism does fail and food goes down the "wrong throat."

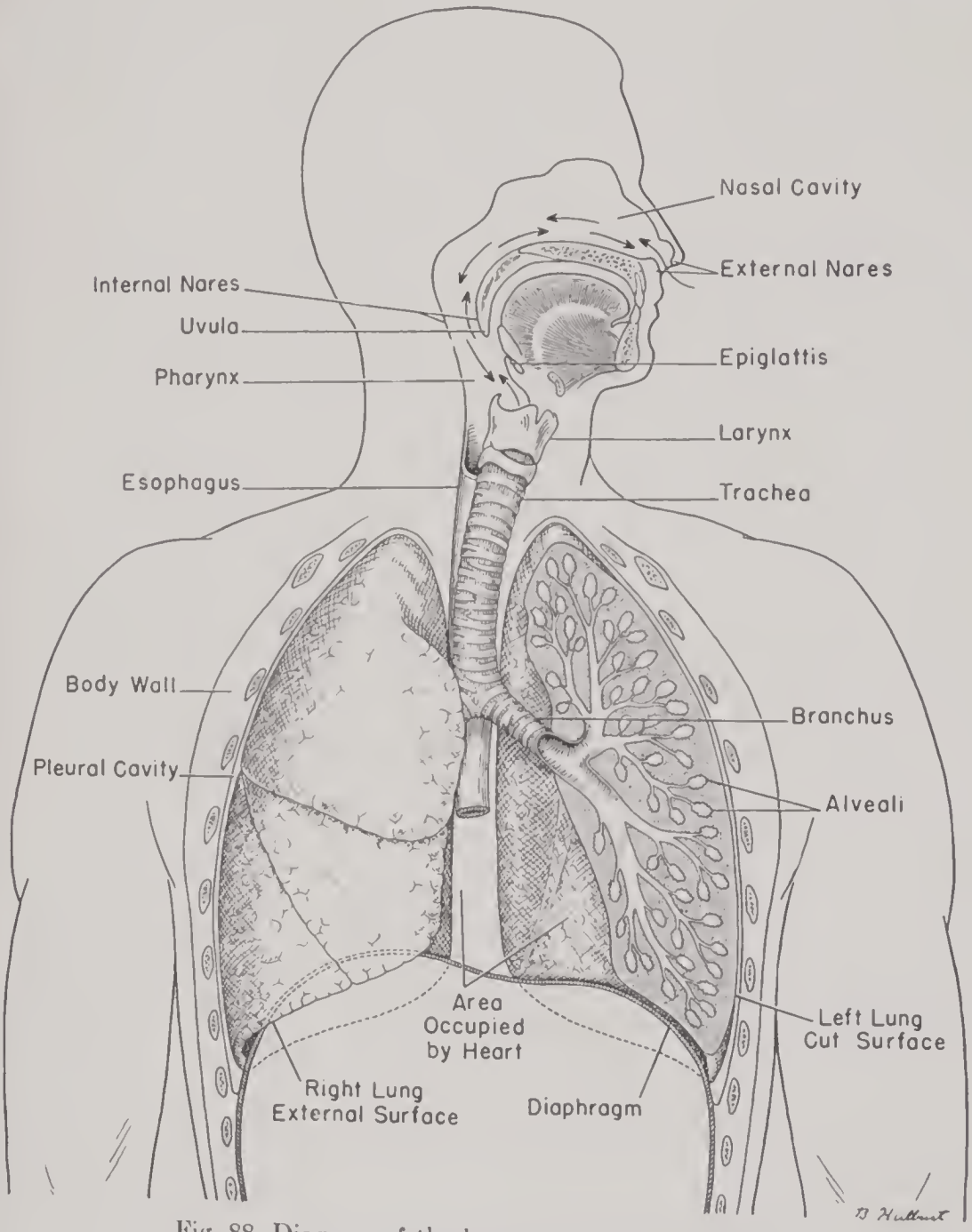


Fig. 88. Diagram of the human respiratory system.

The **larynx,** or voice box (seen on the outside as the Adam's apple), contains the vocal cords, folds of epithelium which vibrate as air passes over them, thereby producing sounds. Muscles adjust the tension on the cords to produce sounds of varying pitch. The **trachea,** or windpipe, may be distinguished from the esophagus by the rings of cartilage imbedded in its walls to hold it open. During inspiration the pressure of air in the trachea is less than atmospheric pressure, and without the cartilaginous rings the trachea would collapse.

At the level of the first rib the trachea branches into two cartilaginous

bronchi, one going to each lung. Inside the lung, each bronchus branches into bronchioles, which in turn branch repeatedly into smaller and smaller tubes leading to the ultimate cavities, the **air sacs.** In the walls of the smaller vessels and the air sacs are minute, cup-shaped cavities, known as **alveoli,** just outside of which are thick networks of blood capillaries. The walls of the alveoli are thin and moist, enabling gas molecules to pass easily through them into the capillaries. The total alveolar surface, across which gases may diffuse, has been estimated to be greater than 1000 square feet—more than fifty times the area of the skin.

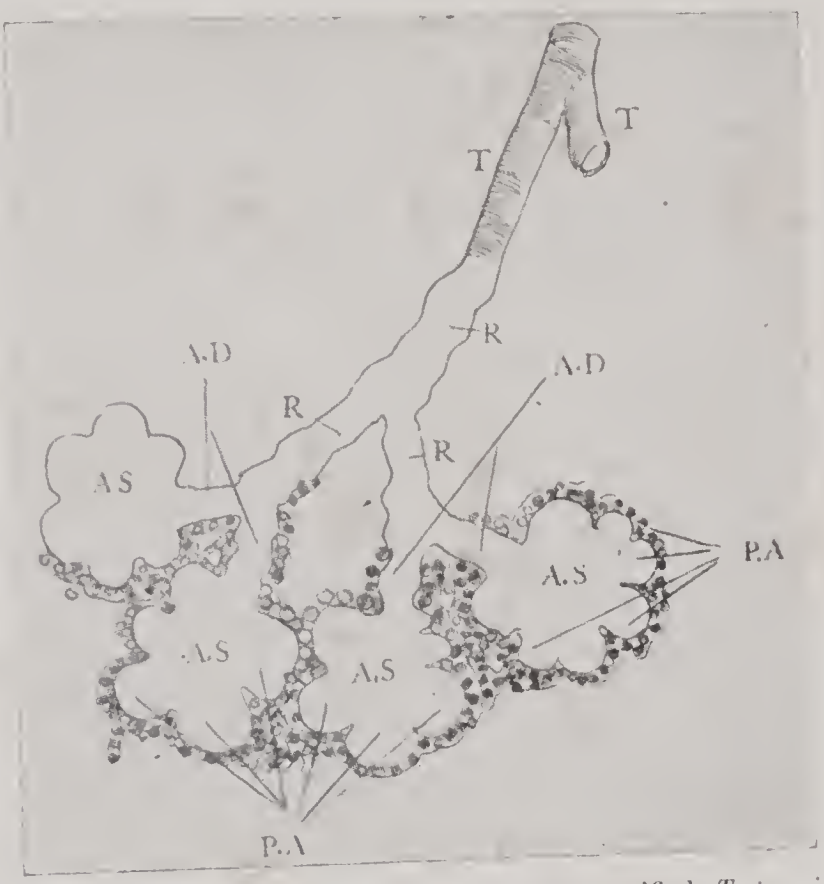


Fig. 89. Diagram of a small portion of a lung, highly magnified. *T*, terminal bronchiole; *A.S.*, air sacs; *P.A.*, pulmonary alveoli. *R* and *A.D.* indicate the fine ducts connecting the bronchioles and the air sacs. Note the small, round, red blood cells in the capillaries surrounding the alveoli (Best and Taylor: The Living Body, Henry Holt and Co., Inc.)

The trachea or bronchus, examined microscopically, is seen to consist of an inner layer of epithelium, an outer layer of connective tissue, and a middle layer containing the cartilaginous rings and smooth muscle fibers. (In a person suffering from asthma these smooth muscle fibers contract abnormally and reduce the size of the passage, thus making breathing difficult.) The lining epithelium secretes mucus and contains ciliated cells. These cilia beat constantly in one direction, so that when solid particles, such as dust, land on the moist surface, they are trapped in the mucus and carried by the beating of the cilia back up to the pharynx. This is an important defense against inhaled bacteria.

As the bronchioles and sub-branches of the respiratory passages become smaller, the walls become thinner, the cartilage layer disappears, and the ciliated cells are replaced by flat pavement epithelium. The walls of the alveoli are composed of just one layer of these flat epithelial

cells, and in some regions even these may be lacking, so that the air in the alveoli is in direct contact with the capillaries (Fig. 89). In between the alveoli and holding them in place are strands of elastic connective tissue, which make the lung pliable. Lungs are so elastic that when they are freshly removed from an animal they may be blown up like a balloon through the trachea. When the pressure is released, the elasticity of the stretched lung deflates it and expels the air that has been blown in. The lung is supplied both with motor nerves, which go to the smooth muscles in the bronchi and bronchioles, and with sensory nerves which ramify throughout it. Each lung, as well as the cavity of the chest in which the lung rests, is covered by a thin sheet of smooth epithelium called the **pleura.** These are both kept moist, enabling the lung to move in the chest cavity during breathing without undue friction.

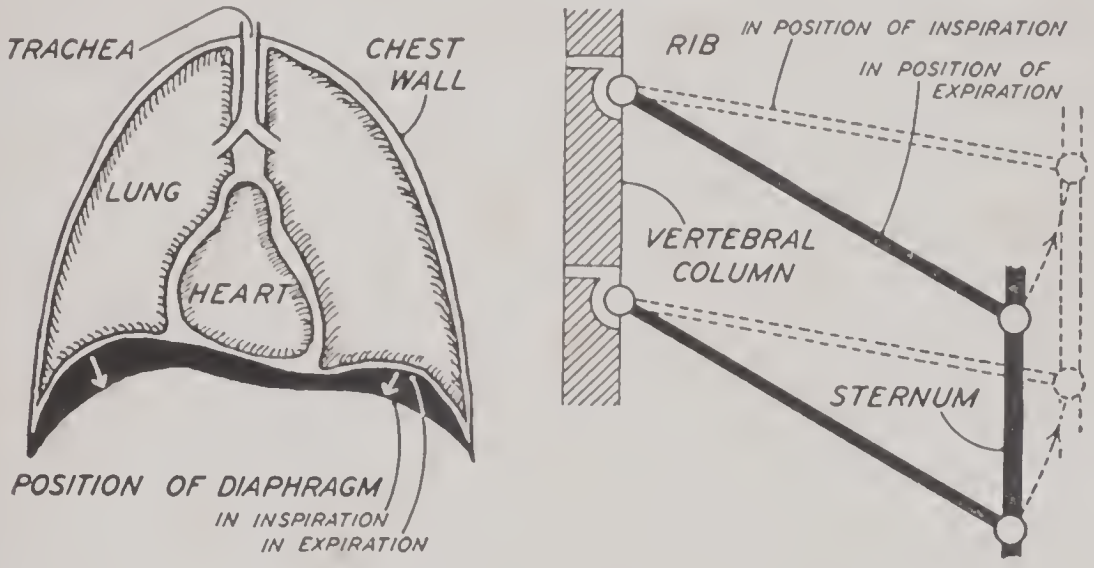


Fig. 90. *A*, Contraction of the diaphragm in inspiration causes the diaphragm to descend (indicated by white arrows). The resulting increase in chest volume is indicated in black. A corresponding volume of air is drawn into the lungs. *B*, Diagram of the movements of the ribs in breathing. The elevation of the front ends of the ribs (by the chest muscles) causes an increase in the front to back dimension of the chest, a corresponding increase in the chest volume, and the intake of an equal amount of air. (Carlson and Johnson: The Machinery of the Body, 3rd ed., published by University of Chicago Press.)

The pressure in the pleural cavity (that between the two sheets of pleura) is generally less than that of the outside atmosphere, because the elasticity of the lungs tends to make them pull away from the chest wall, setting up a partial vacuum in the pleural cavity. When these pleural linings become inflamed, they secrete a fluid which accumulates in the cavity between the lung and the chest wall—a condition known as pleurisy. It is sometimes necessary in cases of severe tuberculosis to collapse one lung and give the infected tissues a chance to rest. This is done by puncturing the chest wall and letting sterile air flow into the pleural cavity; the lung then collapses, owing to its own elasticity.

The chest cavity is closed and has no communication with the outside atmosphere or with any other body cavity. It is bounded on the top and sides by the chest wall, containing the ribs, and on the bottom by a strong, dome-shaped sheet of skeletal muscle, the **diaphragm** (Fig. 88).

4. The Mechanics of Breathing. It is necessary to keep clear the distinction between respiration—the exchange of gases between a cell and its environment (which in man consists of the three phases of external respiration, transportation by the blood stream, and internal respiration)—and **breathing,** which is simply the mechanical process of taking air into the lungs (inspiration), and letting it out again (expiration). Since the lung capillaries are constantly removing oxygen from and putting carbon dioxide into the air in the alveoli, the need for replacing the air in the lungs is obvious. In man the breathing cycle of inspiration followed by expiration is repeated about fifteen to eighteen times a minute.

In human beings and other mammals the ribs, chest muscles and diaphragm are so constructed and arranged as to be easily movable, enabling the volume of the chest cavity to be increased or decreased at will. When it is necessary to increase it, during inspiration, the rib muscles contract, drawing the front ends of the ribs upward and outward, an action made possible by the hingelike connection of the ribs with the backbone (Fig. 90). At the same time the floor of the chest cavity, the diaphragm, contracts, decreasing its convexity and consequently enlarging the cavity. Because the space is closed, this increase in volume results in a lowering of the pressure in the lungs, and when it falls below atmospheric pressure, air from the outside rushes in through the trachea and its branches to the air sacs and alveoli.

That air is expelled from the lungs in expiration is due primarily to the elasticity of the lungs, but to some extent to the weight of the chest wall. During inspiration the lungs are distended as they are filled with air. When the rib muscles relax, the ribs are permitted to return to their original position, and the simultaneous relaxation of the diaphragm permits the abdominal organs to push it back up to its previous convex shape. These factors decrease the chest volume and allow the distended, elastic lungs to contract and expel the air which had been inhaled.

During muscular exercise this passive expiration of the relaxing rib and diaphragm muscles is not rapid enough to expel the air before the next inspiration must start, so that the size of the chest cavity is reduced by muscular contraction. Besides the muscles which raise the ribs for inspiration there is another set, with fibers going at right angles to the first, which lowers the front ends of the ribs and thus decreases the thoracic volume. The muscles of the abdominal wall also contract, squeezing the abdominal organs up against the diaphragm, and further hastening the elastic contraction of the lungs. The chest walls never squeeze the lungs or forcibly expel the air; the decrease in the size of the thoracic cavity simply permits the lungs to contract by means of their own elasticity. Coughing and sneezing are types of forced expirations in which a vigorous contraction of the muscles of the abdominal wall push the abdominal viscera against the diaphragm, decreasing the thoracic volume suddenly, and causing a rapid expulsion of air from the lungs.

The trachea, pharynx and other air passages play no active, muscular

part in the process of breathing; they function simply as conduction channels. In certain cases of obstruction of the throat it is necessary to make an artificial opening in the neck to carry the air to the trachea; the breathing movements then occur normally.

Air pressure within the lungs changes with each breathing movement. In between breaths the pressure in the lungs is the same as atmospheric pressure, since there is free communication between the outside air and that of the interior. As inspiration starts, there is a slight decrease in the air pressure within the lungs to 1 or 2 mm. of mercury below atmospheric. This drop in pressure causes the air to enter the lungs. Toward the end of inspiration the newly entered air has equalized the pressure. As expiration begins, the elasticity of the lungs compresses the air within the lung cavities until the pressure rises to 2 or 3 mm. of mercury above atmospheric; consequently, air passes out of the lungs. Of course, by the end of expiration, pressure within the lungs is back to atmospheric pressure.

5. The Quantity of Air Respired. A man at rest breathes in and out only about 500 cc. (approximately a pint) of air with each breath. When these 500 cc. have been expelled, however, another 1.5 liters or so can be expelled by contracting the abdominal muscles. After this there still remains about 1 liter of air which cannot be expelled. During normal breathing, therefore, a reserve of some 2.5 liters of air remains in the lungs, with which the 500 cc. are mixed. After a normal inspiration of 0.5 liter, it is possible, by inspiring deeply, to take in about 1.5 liters more, and during exercise one can increase the amount of air inspired and expired with each breath, from 0.5 liter to 3.5 liters. But even in strenuous exercise the full sevenfold increase is seldom used; instead, an increased rate of breathing occurs. If one breathes in as deeply as possible and then breathes out as completely as possible into some device for measuring air volume, he will expel about 3500 cc. of air. This total, known as the **vital capacity,** is usually large in trained athletes; in certain heart and lung diseases it may be reduced considerably below normal.

If any air at all has been drawn into the lungs, enough will remain to cause them to float if, at death, they are removed from the body. But a stillborn child, never having drawn a breath, has lungs which sink when placed in water.

Although about 500 cc. of air are breathed in with each inspiration, only some 350 cc. actually reach the alveoli, because the last 150 cc. inhaled remain in the larger air passages, where no exchange of gases between lungs and blood stream can occur. This air is the first to be pushed out with the next expiration. The last 150 cc. expelled from the alveoli with each breath also remain in these tubes, and this air, although laden with carbon dioxide, is the first to be drawn into the alveoli on the next breath. With each breath then, only about 350 cc. of new air reach the lungs to mix with the 2½ liters already there. The 150 cc. of space in the air passages is known as "dead space." If the dead space is increased (by breathing through a long tube, such as a garden hose) the air going to the lungs will soon be depleted of its oxygen, with fatal results.

6. Composition of Alveolar Air. Because the lungs are not completely emptied and filled with each breath, alveolar air has a slightly different composition from atmospheric air (Table 5): it contains less oxygen and more carbon dioxide. A sample of essentially alveolar air can be collected at the end of a maximum expiration. Expired air has had less than one quarter of its oxygen removed and can be breathed over again.

A poorly ventilated room feels "stuffy," not because of a low oxygen content or high carbon dioxide content, but because of the increased water vapor content and high temperature of air that is breathed over and over.

7. Exchange of Gases in the Lungs. Oxygen passes from the alveoli to the pulmonary capillaries, and carbon dioxide passes in the reverse direction, simply by the physical process of diffusion: each gas passes from a region of higher concentration to one of lower concentration.

Table 5. Percentage Composition of Atmospheric and Alveolar Air

	Atmospheric Air	Alveolar Air
Nitrogen	79.0	80.3
Oxygen	20.96	14.2
Carbon dioxide	0.04	5.5
Water vapor	Variable	Almost saturated

The extremely thin alveolar epithelium offers little resistance to the passage of the gases, and since there is normally a greater concentration of oxygen in the lung alveoli than in the blood arriving in the lungs by the pulmonary artery, oxygen diffuses from the alveoli into the capillaries. Similarly, the concentration of carbon dioxide in the blood in the pulmonary artery is normally higher than in the lung alveoli, so that carbon dioxide diffuses from the lung capillaries into the alveoli. In contrast to the cells lining the intestine, which can take a substance from the intestinal cavity and pass it into the blood, where the concentration of that substance may be higher, the alveolar epithelium is unable to move either oxygen or carbon dioxide against a diffusion gradient.

Because the cells of the alveoli cannot force oxygen into the blood, whenever the concentration of that gas in the alveoli drops below a certain value, the blood passing through the lungs cannot take up enough to meet the body's needs and the symptoms of altitude sickness—nausea, headache and delusions—appear. Altitude sickness begins to occur at about 15,000 feet, or even lower with some persons. People can become acclimated to living at high altitudes by increasing the number of red cells in the blood, but no one can live much above 15,000 feet without a supply of oxygen to draw upon. At about 35,000 feet the pressure is so low that even when a man breathes pure oxygen he cannot get enough to supply his body. For this reason airplanes flying at that height must be made airtight and pumps must be provided to maintain the air pressure equal to that at a lower altitude, usually 8000 feet.

In the capillaries of the tissues all over the body, where internal res-

piration takes place, diffusion is again the force which moves oxygen from the capillaries to the cells, and carbon dioxide from the cells to the capillaries. Because of the constant burning of glucose and other substances in the cells, there is a continual production of carbon dioxide and utilization of oxygen. Consequently, the concentration of oxygen is always lower, and the concentration of carbon dioxide is always higher, in the cells than in the capillaries.

Throughout the system, from lungs to blood to tissues, oxygen moves from a region of high concentration to one of lower concentration, and is finally used in the cells; carbon dioxide moves from the cells, where it is produced, through the blood to the lungs and out, always towards a region of lower concentration.

8. Transportation of Oxygen by the Blood. At rest, the cells of a man's body need about 300 liters of oxygen every twenty-four hours, or 250 cc. per minute. With exercise or work this requirement may increase to as much as ten or fifteen times that amount. If oxygen were delivered to the tissues simply dissolved in plasma, blood would have to circulate through the body at a rate of 180 liters per minute to supply enough oxygen to the cells at rest—for oxygen is not very soluble in plasma. Actually, when a man is resting, blood circulates at about 5 liters per minute and supplies all the oxygen the cells need. The difference between 180 and 5 liters per minute is due to the action of hemoglobin.

Hemoglobin is the pigment in red blood cells which carries the burden of transporting nearly all the oxygen and most of the carbon dioxide. The importance of its role can be inferred from the fact that only about 0.2 cc. of oxygen and 0.3 cc. of carbon dioxide will dissolve in 100 cc. of blood plasma, yet 100 cc. of whole blood can carry about 20 cc. of oxygen and 30 to 60 cc. of carbon dioxide.

Approximately 2 per cent of the oxygen in the blood is dissolved in the plasma; the rest is carried in combination with the hemoglobin. After oxygen enters the capillaries in the lungs, it diffuses into the red cells from the plasma and unites with hemoglobin—that is, one molecule of oxygen unites with one molecule of hemoglobin to form a molecule of oxyhemoglobin:

$$\underset{\text{Hemoglobin}}{Hb} + O_2 \rightleftarrows \underset{\text{Oxyhemoglobin}}{HbO_2}$$

The arrows indicate that the reaction is reversible: it can go in either direction, depending on local conditions. Hemoglobin would, of course, be of little value to the body if it could only take up oxygen and not give it off where needed. The reaction goes to the right in the lungs, forming oxyhemoglobin, and to the left in the tissues, releasing oxygen. The difference in color between arterial and venous blood is due to the fact that oxyhemoglobin is a bright scarlet, whereas hemoglobin is purple.

The combination of oxygen with hemoglobin and the breakdown of oxyhemoglobin are controlled by two factors: primarily, the amount of oxygen present, and, to a lesser extent, the amount of carbon dioxide present. In the lungs the concentration of oxygen is relatively high,

and oxyhemoglobin is formed. After leaving the lungs the blood passes through the heart and arteries, where there is little change in the oxygen concentration, to the tissues, where the oxyhemoglobin is exposed to an environment with little oxygen. It consequently breaks down, releasing the oxygen to diffuse to the tissue cells. The role of carbon dioxide in controlling this reaction is less evident, and since the chemical details are quite complex, we shall not consider it. The important thing to realize is that the more carbon dioxide the blood contains, the more acid it is, and that the oxygen-carrying capacity of hemoglobin is less in an acid solution.

The factor which actually determines the direction and rate of diffusion is the pressure or "tension" of the particular gas. In a mixture of gases each one exerts, independently of the others, the same pressure it would exert if it were present alone. In the air at sea level, where the total pressure is about 760 mm. of mercury, oxygen exerts one fifth, or 150 mm., of the pressure. The partial pressure or tension of oxygen in the atmosphere is, then, 150 mm. of mercury. Since the alveolar air has less

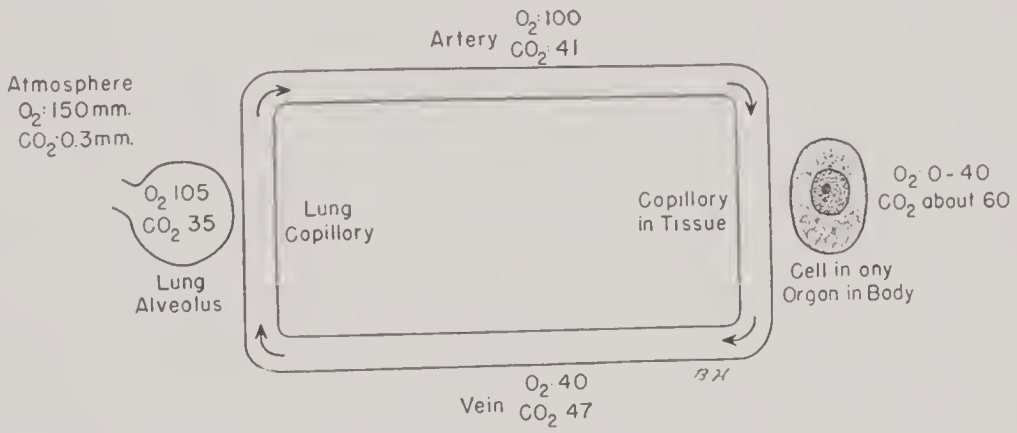


Fig. 91. Diagram of the tensions, in millimeters of mercury, of oxygen and carbon dioxide in lungs, vessels and tissues, illustrating the diffusion gradients responsible for the movements of the molecules.

oxygen than atmospheric air, the tension of oxygen in the alveoli is about 105 mm. Blood passes through the lung capillaries too rapidly to become completely equilibrated with the alveolar air, so that the oxygen tension in the arterial blood is about 100 mm. (Fig. 91). The oxygen tension in the tissues varies from 0 to 40 mm., with the result that oxygen diffuses out of the capillaries into the tissues. Not all the oxygen leaves the blood, however; blood passes through the capillaries too rapidly for a complete equilibrium to be reached, and the tissues usually have some residual oxygen. The venous blood returning to the lungs has an oxygen tension of about 40 mm. of mercury. At the oxygen tension of arterial blood (100 mm.), each 100 cc. contains about 19 cc. of oxygen. At the oxygen tension of venous blood (40 mm.), each 100 cc. contains 12 cc. of oxygen. The difference of 7 cc. represents the amount of oxygen delivered to the tissues by each 100 cc. of blood. Thus the 5 liters of blood in the body can deliver 350 cc. of oxygen on each circuit.

9. Transportation of Carbon Dioxide by the Blood. The transportation of carbon dioxide poses a special problem to the body, because, when

carbon dioxide dissolves, it is quickly converted into carbonic acid:

$$CO_2 + H_2O \rightleftarrows H_2CO_3$$

The cells of the body produce, at rest, about 200 cc. of carbon dioxide per minute. If this were simply dissolved in plasma (which can hold in solution only 4.3 cc. of carbon dioxide per liter), blood would have to circulate at a rate of 47 liters per minute instead of 4 or 5. Furthermore, this amount of carbon dioxide would give the blood a *p*H of 4.5, and cells are able to survive only within a narrow range on the alkaline side of neutrality (between about *p*H 7.2 and 7.6). The fact that blood can carry as much carbon dioxide as it does and that the difference in *p*H between arterial and venous blood is only a few hundredths of a *p*H unit, is again due largely to hemoglobin. Some of the carbon dioxide is carried in a loose chemical union with hemoglobin, and a small amount is present as carbonic acid, but most of the latter is converted into bicarbonates through neutralization of the carbonic acid by sodium or potassium ions released when oxyhemoglobin is changed into hemoglobin. The chemical details of this process are complicated and beyond the scope of this book, but it is interesting to realize that in the course of evolution, a single chemical, hemoglobin, has been produced, with all the necessary characteristics for assisting respiration: the ability to transport oxygen, to transport carbon dioxide, and to keep the *p*H of the blood constant throughout the transportation process.

Carbon dioxide passes from tissues to blood to lungs because it must diffuse from a region of high tension to one of lower tension. The carbon dioxide tension in the tissues is about 60 mm. of mercury; in the venous blood, about 47 mm., and in the alveoli, about 35 mm. of mercury. Arterial blood has a carbon dioxide tension of about 41 mm. of mercury, so that the blood contains a great deal of carbon dioxide after it has passed through the lungs, although each liter of blood in passing from the tissues to the lungs is relieved of about 50 cc. of carbon dioxide. The process of converting carbon dioxide into carbonic acid in the capillaries of the tissues, and of converting the carbonic acid back into carbon dioxide to diffuse out in the lung capillaries, is speeded up 1500 times by a special enzyme called **carbonic anhydrase.**

When the removal of carbon dioxide by the lungs is interfered with, as in pneumonia, its concentration (really bicarbonates and carbonic acid) in the blood increases, and the term **acidosis** is applied to the condition of the blood. This does *not* mean that the blood is actually acid (it is still on the alkaline side of neutrality), but there is a decrease in the alkaline reserves of the blood (chiefly sodium). When the alkaline reserves are exhausted, the blood is no longer able to remain alkaline, but changes its *p*H, and the cells of the tissues die because of exposure to the acid blood. Acidosis also occurs in diabetes. Here, however, the trouble is not due to a failure to remove the carbon dioxide in the lungs, but to an overproduction by the tissues of acids because of an abnormal carbohydrate metabolism.

10. Asphyxia. Asphyxia results whenever there is an interruption in the delivery of oxygen to the tissues or a failure in the utilization of

oxygen by the tissues. Therefore, the cause of asphyxia may lie in the lungs, blood or tissues. In drowning, the lung alveoli become filled with water, and in pneumonia they become filled with tissue fluid, bringing about asphyxia from lack of oxygen. In carbon monoxide poisoning, asphyxia results because the hemoglobin of the blood unites with carbon monoxide instead of oxygen and so is unavailable for transporting oxygen to the cells. In cyanide poisoning, asphyxia is caused by the inactivation of one of the enzymes present in each cell (cytochrome oxidase) which is an important link in the chain of enzymes responsible for the utilization of oxygen by the tissues.

11. Artificial Respiration. In cases of near-drowning or of electric shock the respiratory center may be temporarily impaired, causing the breathing movements to cease, although the person is still alive and his heart beating. A person in such dire straits will soon die unless artificial respiration is substituted for the breathing movements until they can be resumed naturally. A number of mechanical devices called pulmotors have been invented to pump air into the lungs, but they are seldom available when needed. The Schaefer method of artificial respiration, which requires no apparatus, is a simple and effective procedure. Victims of drowning accidents sometimes require an hour or more of artificial respiration.

12. The Control of Breathing. Since the needs of the body for oxygen are different at rest and at work, the rate and depth of breathing must change automatically to meet varying conditions. During exercise the oxygen consumption by muscles and other tissues may increase four or five times.

Breathing requires the coordinated contraction of a great many separate muscles, which is achieved by the **respiratory center,** a special group of cells in the part of the brain known as the medulla. From this center, volleys of nervous impulses pass out rhythmically to the diaphragm and rib muscles, resulting in their regular and coordinated contraction every four or five seconds. Under ordinary conditions the breathing movements are automatic and occur without our voluntary control. However, when the nerves to the diaphragm (the phrenic nerves) and the rib muscles are cut or destroyed, as in infantile paralysis, breathing movements stop at once. Of course, we can voluntarily change the rate and depth of breathing. We can even hold our breath for awhile, but we cannot hold it long enough to do any serious harm—the automatic mechanism takes over and brings about an inspiration.

The question naturally occurs: Why does the respiratory center give off this volley of impulses periodically? Through a series of experiments it has been determined that if the connections of the respiratory center with all other parts of the brain are cut—that is, if the sensory nerves and those from the higher brain centers are severed—the center sends out a constant stream of impulses, and the breathing muscles contract and stay that way. The respiratory center, then, if left to its own devices, causes a complete contraction of the breathing muscles. If either the sensory nerves or the nerves from the higher centers of the brain are left intact, however, the breathing movements continue in normal

fashion. This means that for normal breathing to occur, the respiratory center must be inhibited periodically, so that it stops sending out impulses which cause contraction of the muscles. In this way the normal alternation of inspiration and expiration occurs. At the height of an inspiration the walls of the lungs are stretched. This stimulates pressure-sensitive nerve cells there, which send impulses to the brain inhibiting the respiratory center and bringing about the following expiration.

Many other nervous pathways, connected with the respiratory center, either stimulate or inhibit it. Severe pain in any part of the body causes a reflex acceleration of breathing. Also, both the larynx and the pharynx have receptors in their linings which, when stimulated, send impulses to the respiratory center to inhibit breathing. These are valuable protective devices. When an irritating gas, such as ammonia or acid fumes, passes down the respiratory tract, it stimulates the receptors in the larynx, which, by sending impulses to the respiratory center to inhibit breathing, bring about an involuntary "catching of the breath." This prevents the harmful substance from entering the lungs. Similarly, when food accidentally passes into the larynx, it stimulates receptors in the lining of that organ to send inhibitory impulses to the respiratory center. This momentarily stops breathing so that the food does not enter the lungs, where the lining epithelium is exceedingly delicate and vulnerable to serious damage by foreign substances. It is impossible, because of this protective device, absentmindedly to take a breath and swallow at the same time. Thus the respiratory center and its associated nerves provide a device for keeping the rate of breathing constant.

During exercise the rate and depth of breathing must increase, and a special adjustment of the rate of breathing to the momentary needs of the body for oxygen is necessary. If the rate of breathing is not fast enough, carbon dioxide accumulates in the alveoli until there is no longer a lower concentration of carbon dioxide in the lungs than in the blood. Thus, its diffusion from blood to alveoli ceases, and its concentration in the blood increases correspondingly. The respiratory center of the brain is especially sensitive to changes in the concentration of carbon dioxide in the blood. Increases in concentration there—for example, during muscular exercise—stimulate it to send out impulses to the muscles of breathing, increasing the rate and depth of breathing until the carbon dioxide content of the lungs and blood is brought back to normal, so that the respiratory center is no longer stimulated. Small changes in the concentration of carbon dioxide (as little as 0.2 per cent) can double the breathing rate.

This mechanism also works in reverse. If a person voluntarily takes a series of deep inhalations and exhalations, he reduces the carbon dioxide content of his alveolar air and blood to such a degree that when he stops breathing deeply, all breathing movements cease until the carbon dioxide in the blood again builds up to normal. The first breath of a newborn child is initiated largely by this mechanism. Immediately after a baby is born and separated from the placenta, the carbon dioxide content of its blood increases, stimulating the respiratory center to send nerve impulses to the diaphragm and rib muscles to contract in the first breath. Sometimes, when a newborn infant has difficulty in taking its

first breath, air containing 10 per cent carbon dioxide is blown into its lungs, to set off this mechanism.

Experiments have shown that an increase in the carbon dioxide content, rather than a decrease in the oxygen content, of the blood is primarily effective in stimulating the respiratory center. If a man is placed in a small, air-tight chamber so that he breathes and rebreathes the same air, the oxygen in the air gradually decreases. If a chemical is placed in the chamber to absorb the carbon dioxide as fast as it is given off, so that it does not increase in the lungs and blood, the man's breathing accelerates only slightly, even if the experiment is continued until the oxygen content is greatly reduced. If, however, the carbon dioxide is not absorbed, but is allowed to accumulate, the breathing will be greatly accelerated, causing discomfort and a choking sensation in the subject. When he is supplied with air containing the normal amount of oxygen, but with an increased carbon dioxide content, there is again an acceleration of breathing. Obviously, it is primarily the accumulation of carbon dioxide, not an oxygen deficiency, which stimulates the respiratory center.

As additional protection against the failure of the body to respond properly to changes in the carbon dioxide and oxygen content of the blood, still another control has evolved. At the base of each internal carotid artery is a small swelling, called a carotid sinus, containing receptors sensitive to changes in the chemicals of the blood. If the carbon dioxide increases, or the oxygen decreases, these receptors are stimulated to send nerve impulses to the respiratory center in the medulla, increasing its activity.

13. The Effects of Training. The exercises and practice which an athlete performs in training increase his ability to do a certain task. First, the muscles increase in size with use and become stronger (owing to growth in the individual muscle fibers, not to an increase in the number of fibers). Second, as one performs a certain act repeatedly, he learns to coordinate muscles and to contract each one just enough and no more to produce the desired result, with consequent savings in energy. Third, changes occur in the circulatory and respiratory systems. The heart of a trained athlete is somewhat larger than normal and beats more slowly at rest. During exercise it pumps a greater volume of blood, more by increasing the strength of the beat than by increasing its rate. In addition, an athlete breathes more slowly and more deeply than the average person, and during exercise he increases the amount of air breathed by increasing the depth of his breathing, rather than by stepping up the rate. This is the more efficient way of doing it.

14. The Evolution of the Human Lungs. The lungs of man and other mammals have had a long evolutionary history. The earliest suggestion of a lung is found in certain types of fish. Some ancestral, fossil fish developed an outgrowth of the anterior end of the digestive tract, and in the line of fishes that eventually gave rise to the land vertebrates, this outgrowth became a lung. In other fishes it became a swim bladder—that is, an appendage which facilitates floating, though it may function as a respiratory organ (Fig. 92). The swim bladder is usually single, although it may be paired and exhibit great variation in size and

shape. In some fish it has lost its connection with the digestive tract. The cells at the anterior end of the swim bladder have the ability, found nowhere else in the animal kingdom, to secrete oxygen from the blood into the internal cavity. Another set of cells at the posterior end remove oxygen from it for return to the blood stream. By thus "pumping"

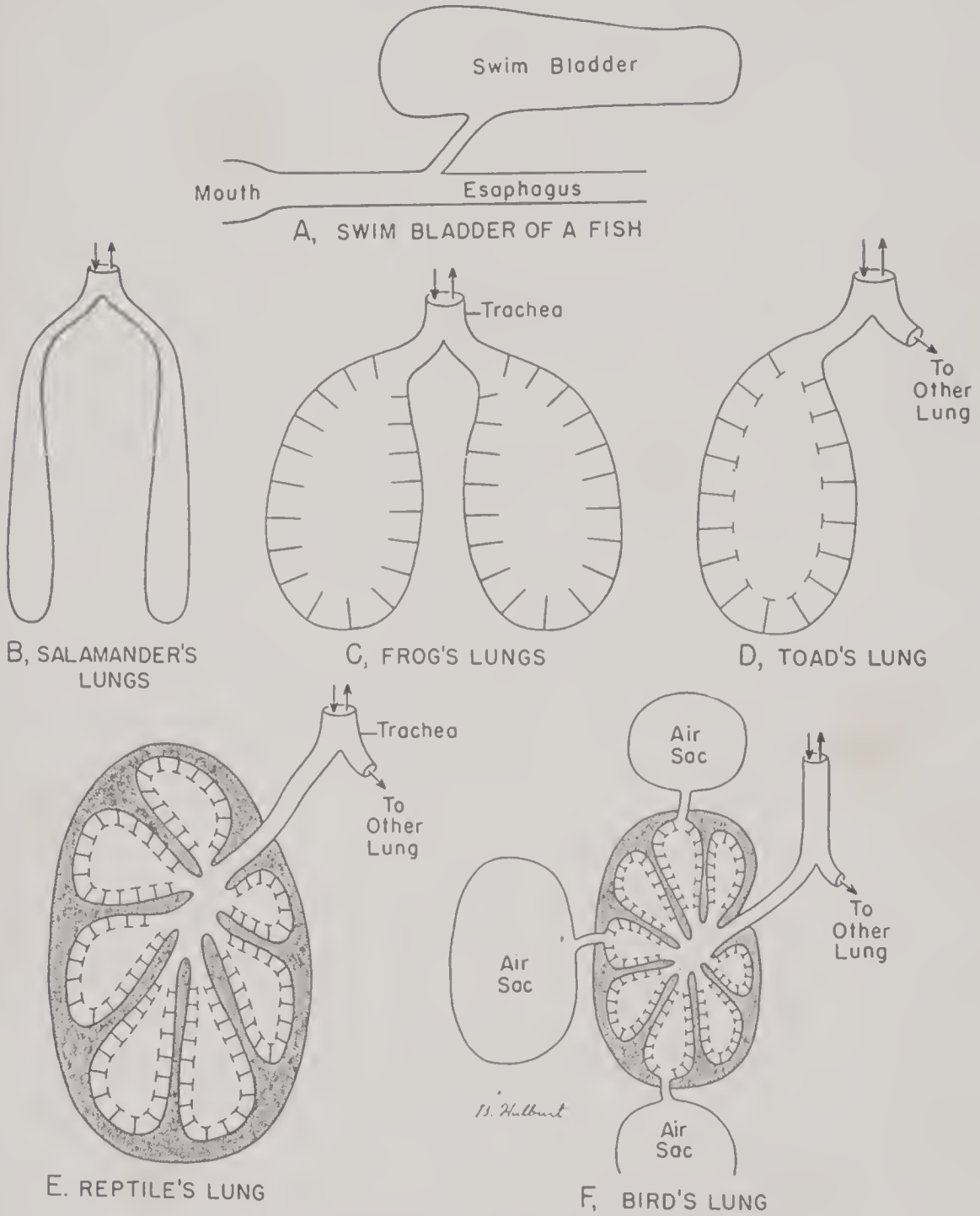


Fig. 92. Some stages in the evolution of the lungs.

oxygen in or out of these swim bladders, the fish maintain a certain depth in the water without muscular effort. Several fish are even equipped with a series of bones that connect this organ with the internal ear and presumably act as a depth gauge.

The swim bladder is also an organ for the production of sounds. A few fish, such as the toadfish and sea robin, are able to make a noise, by a muscle attached to the swim bladder which causes it to vibrate.

Close relatives of the fish that gave rise to the land vertebrates are

the lungfish, a few of which have survived to the present time in the headwaters of the Nile and the Amazon, and in certain Australian rivers. These animals live in streams that dry up periodically, and during the dry seasons they remain in the mud of the stream bed, breathing by means of their swim bladders. They are also equipped with gills, by means of which they breathe when swimming. The swim bladders of these fish are simple sacs, single in some forms, paired in others. In contrast to those of other fish, they are equipped with a pulmonary artery. The lungs of the most primitive amphibians, the mud puppies, are two long simple sacs, covered on the outside by capillaries. Frogs and toads have folds on the inside of the lung sac which increase the available

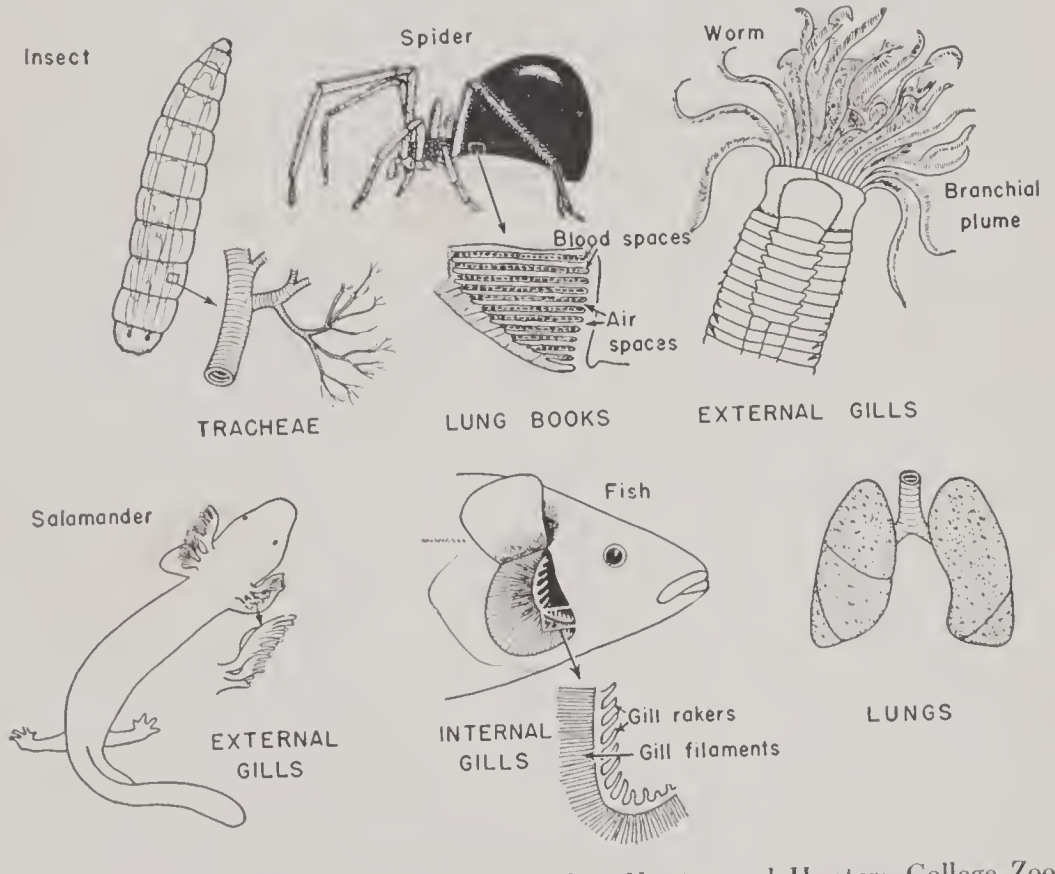


Fig. 93. Respiratory devices in certain animals. (Hunter and Hunter: College Zoology.)

respiratory surface (Fig. 92). Since frogs have no diaphragm or rib muscles, their method of breathing is quite different from man's and depends on the action of valves in the nostrils and muscles of the throat. With the nose valves open, the floor of the mouth cavity is drawn down and air is taken into the mouth. Then the nose valves close, and the throat muscles contract, decreasing the size of the mouth cavity and forcing the air back into the lungs. A frog cannot breathe with his mouth open!

The trend in evolution from amphibians on up is toward a greater subdivision of the lung into smaller and smaller sacs, so that the lung structure becomes increasingly complex in reptiles, birds and mammals. The lungs of some lizards—for example, the chameleon—have supplementary air sacs that can be inflated, enabling the animal to swell up—perhaps a protective device to frighten would-be predators. Birds have rather similar sacs at several points throughout the body (Fig. 92) by

which air can be drawn all through the lungs, and completely renewed on each inspiriation. In addition, when the bird is flying and the chest wall must be held rigid to form an anchor for the flight muscles, the air sacs act as a bellows to move air in and out of the lungs. The air sacs, lying between certain flight muscles, are squeezed and relaxed on each stroke of the wing; thus, the faster a bird flies, the more rapid is the circulation of air through the lungs.

15. Respiratory Devices in Other Animals. External respiration in most aquatic animals is carried on by specialized structures called gills. Fish, molluscs (oysters, squids) and many arthropods (shrimps, crabs, spiders, and so forth, but not insects) (Fig. 93) have these organs. Every animal with gills has some arrangement for keeping a current of water flowing over them. In fish, water is taken in through the mouth, passes over the gills, and out the gill clefts. Gills, like the human respiratory organ, have thin walls, and are moist and well supplied with blood capillaries. Oxygen dissolved in the water diffuses through the gill epithelium into the capillaries, and carbon dioxide diffuses in the reverse direction. Fish suffocate in water lacking sufficient dissolved oxygen, such as that in stagnant ponds.

Insects have quite a different system for getting oxygen to the cells. In each section or segment of the body is a pair of holes, called spiracles, from which a tracheal tube extends into the body, branching and rebranching until it reaches each cell (Fig. 93). The body walls of insects pulsate, drawing air into the trachea when the body expands, and forcing air out when the body contracts. Thus, in contrast to a fish or crab, in which blood is brought to the surface of the body to be aerated in a gill, the tracheal system conducts air deep within the insect body, near enough to each cell so that it can diffuse in through the wall of the tracheal tube.

QUESTIONS

1. State exactly what function oxygen performs in the body.
2. What are the parts of the human respiratory system, and how, in detail, are they adapted to their functions?
3. What is the difference between breathing and respiration?
4. What is the special importance of hemoglobin in respiration?
5. What is meant by oxygen "tension"?
6. What is acidosis, and what causes it?
7. What does the respiratory center do, and where is it located? Why must its action be inhibited?
8. Exactly what happens when too much carbon dioxide accumulates in the cells?
9. What has been the outstanding trend in the evolution of the lungs?
10. How do gills operate?
11. How is respiration carried on in insects?
12. Trace the path of an anesthetic such as ether, from the ether cone over the nose to a cell in the brain. List each structure passed and the processes involved.
13. Differentiate between direct and indirect respiration, and between external and internal respiration.

SUPPLEMENTARY READINGS

See the Readings at the end of Chapter 9.

CHAPTER 11

THE DIGESTIVE SYSTEM

FOR the same reasons that simple animals do not need a special system for respiration, they do not need a special set of organs for taking in food. In such animals, food passes directly into the cell or cells, where it is broken down chemically. In the evolutionary process, the higher, more complex animals developed special organs for obtaining food, and, in such forms as the earthworm, the frog, and man, food is digested and taken into the body in organs far removed from the places where it is eventually utilized—the individual cells.

In man the digestive system is a long tube, composed of several separate organs (Fig. 94), which perform three main functions: **ingestion**, **digestion** and **absorption**. Ingestion is simply the mechanical taking in of food through the mouth, chewing and swallowing. Digestion, which follows, is a chemical process—the breakdown, by enzyme action, of large, complex food molecules into simpler, smaller ones which can pass through the wall of the digestive tract. The passage of substances through the wall is called absorption; it can occur only after the food molecules have been digested, because the wall of the digestive tract is a semipermeable membrane. Since digestion occurs almost entirely in the stomach and small intestine, it can occur only after food has been ingested.

I. THE MOUTH CAVITY

Food is ingested through the mouth into the mouth cavity, bounded on the sides by the teeth, gums and cheeks, on the bottom by the tongue, and on the top by the palate. The last, which separates the mouth cavity from the nasal cavity, has an anterior bony part, the hard palate, and a posterior fleshy part, the soft palate. The latter plays a role during swallowing in preventing food from passing up into the nasal cavity. The tongue, teeth and salivary glands, with ducts emptying into the mouth cavity, are all important in ingestion or digestion. The tongue and teeth in man have assumed an additional function, that of speech.

1. The Tongue. The tongue consists of several sets of striated muscles running in different directions, and thus it can move in or out, up or down, or from side to side. Muscles, of course, can only exert a pull, not a push; so that to stick the tongue out, the muscles running up and down and from side to side contract, while the muscles running from front to back relax. By its movements the tongue manipulates the food in such a way that each bit is pushed in turn between the teeth to be chewed. It then shapes the food into a spherical mass, called a bolus, to be swallowed. Swallowing is initiated when the tongue pushes a bolus into the pharynx. The tongue of some animals, such as frogs and ant-

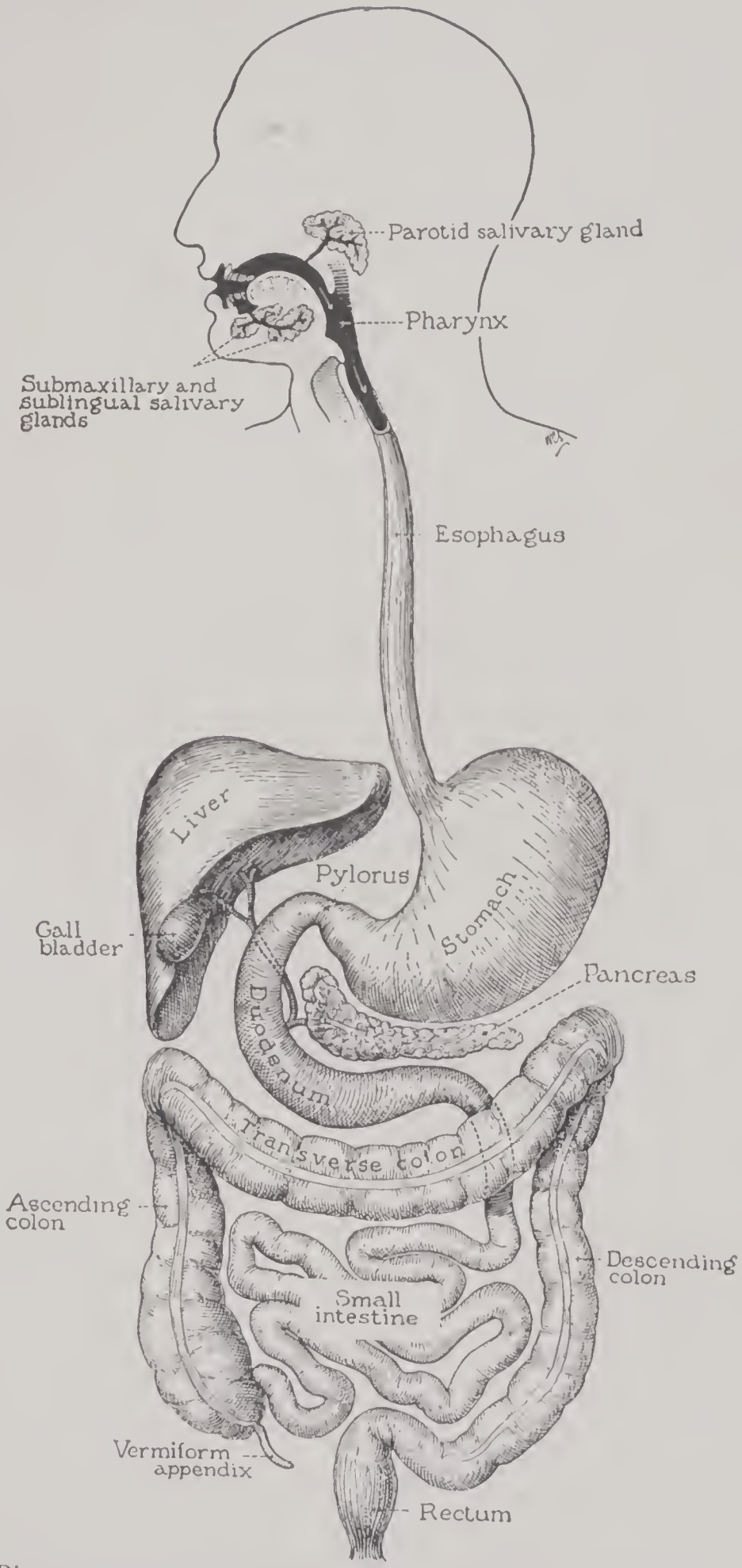


Fig. 94. Diagram of the human digestive system. The liver, which normally covers the stomach and duodenum, has been folded back to reveal these, and to show the gallbladder on its under surface. (Clendening, L.: The Human Body. Copyright 1927, 1945, by Alfred A. Knopf, Inc.)

caters, is long and covered with mucus, enabling them to reach out and catch insects in flight. The surface of the tongue contains groups of sensory cells called taste buds, which analyze substances in solution and make possible our taste sensations.

2. The Teeth. The teeth of all vertebrates serve the common function of breaking food up into smaller particles, but they vary in size and shape according to the diet of the particular animal. Although they are superficially quite different, they have a common pattern (Fig. 95).

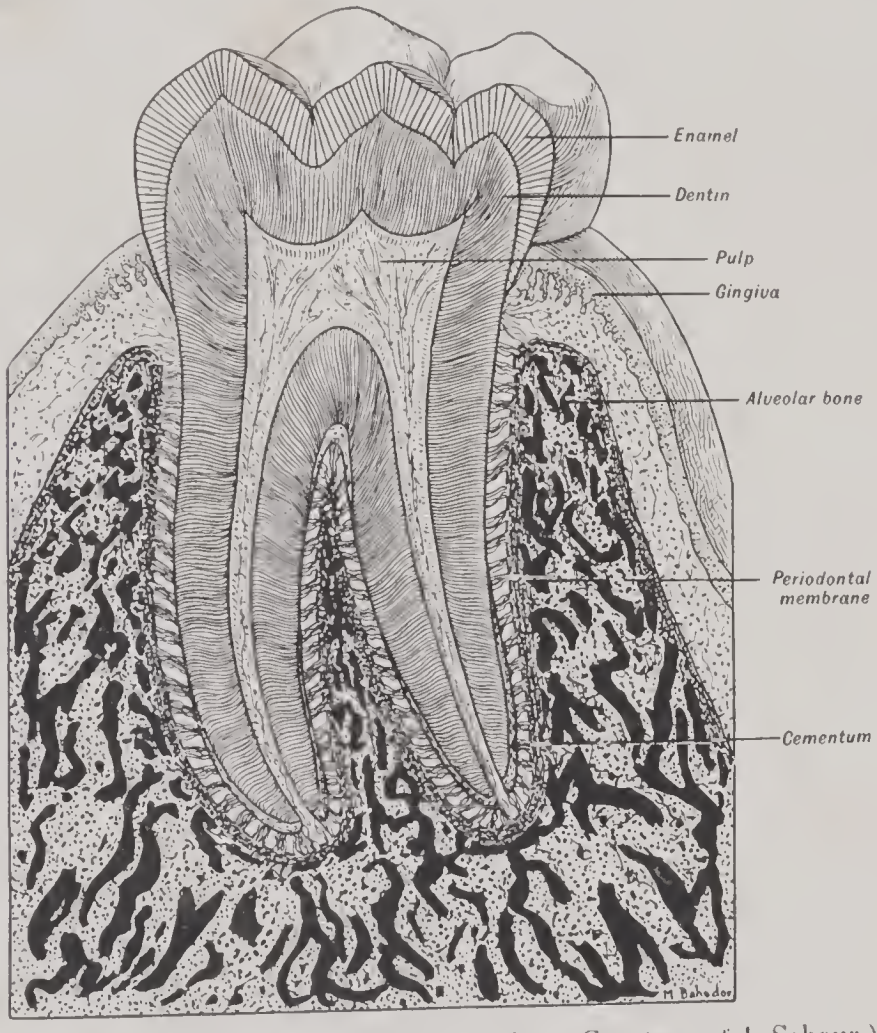


Fig. 95. Diagram of a section through a human molar. (Courtesy of I. Schour.) (Maximow and Bloom.)

The part of the tooth projecting above the gum is called the **crown**, that surrounded by the gum is called the **neck**, and below the neck is the **root**, imbedded in a socket in the jaw bone. Each tooth is composed of several layers, a hard outer one, called **enamel**, an inner layer which is not quite so hard, called **dentine**, and an innermost pulp cavity, filled with blood vessels, nerves and soft tissue, the **pulp**. The enamel covers only the crown and upper part of the neck of the tooth. The tooth is fastened to the jawbone by a substance called **cement**. Dentine resembles bone in its composition and hardness, and consists of about 72 per cent inorganic matter (primarily calcium phosphate) and 28 per cent organic matter. Enamel, the hardest substance in the body, consists of almost 97 per cent inorganic matter.

Unlike the teeth of fish, amphibians and reptiles, which are simple,

pointed cones in all parts of the mouth, the teeth of mammals are not uniform, but are specialized to perform particular functions. The eight front, chisel-shaped teeth, called **incisors,** are used for biting. These are especially large in gnawing animals such as rats, squirrels and beavers. The four cone-shaped **canine** teeth, one in each front corner of the mouth, are used for tearing food. Flesh-eating animals such as wolves and lions have large canine teeth or fangs—in fact, they are called canine or dog teeth because they are so large in dogs. Behind the canine teeth on each side and in each jaw are two **premolars** and three **molars,** with flattened surfaces adapted for crushing and grinding food. In flesh-eating animals the molars are knife-shaped instead of flat and are used in shearing flesh. Vegetarians such as horses and cows have large, flat molars for grinding food and well-developed incisors for cutting off grass. After their upper incisors fall out, sheep and cows crop grass by pulling

Fig. 96. The salivary glands of man and their ducts. G_1, Sublingual gland; G_2, submaxillary gland; G_3, parotid gland. Only the glands of the left side are shown, but each gland is paired. (Carlson and Johnson: Machinery of the Body. 3rd edition, published by University of Chicago Press.)

it with their tongue and upper lip across the cutting edge of the lower incisors.

Since man's ancestors were omnivorous for millions of years, human teeth are relatively unspecialized. The last molar, or wisdom tooth, in man frequently fails to erupt, or, if it comes through the gum, it is often crooked and useless. This defect is due to a trend in the evolution of modern man toward a shortening of the jaws, with a resulting crowding of the teeth, which leaves inadequate space for the last molar. In primitive races, such as the Australian aborigines, this has not occurred. It is quite possible that in another hundred thousand years, man may not have wisdom teeth.

3. The Salivary Glands. To assist the food in moving down the throat, as well as to begin its chemical breakdown, there are two kinds of saliva, secreted by three pairs of salivary glands. One type of saliva is watery, to dissolve dry foods, and the other contains mucus, to lubricate the food as it passes down the esophagus and to make the food particles stick together in a bolus for swallowing. Saliva also protects the lining of the mouth against drying out, cleans it, and facilitates speech by

moistening the tongue so that it does not stick to the roof of the mouth. The three pairs of glands produce about 2 quarts of saliva each day. The **parotid glands** (Fig. 96), located in the cheek just in front of the ear, produce only a watery saliva; the **submaxillary glands,** in front of the angle of the jaw, produce a mixture of watery and mucous saliva, as do the **sublingual glands,** located on the floor of the mouth under the tongue. Each glandular mass weighs about an ounce and is connected to the mouth cavity by a duct.

Saliva is one of the digestive juices; it breaks down food into simple chemicals which can be absorbed by the body. The enzyme **ptyalin,** which transforms starch into maltose, or malt sugar, is one of its components, as is a small amount of maltase, which breaks maltose down further to glucose. Saliva is normally slightly acid, with a *p*H of 6.5 to 6.8, and ptyalin works best in this range. In the very acid condition of the stomach, the action of ptyalin ceases, but because food is swallowed in masses, it takes time for the acid to penetrate, and ptyalin continues to work in the stomach until that happens.

II. MICROSCOPIC ANATOMY OF THE DIGESTIVE TRACT

All the parts of the digestive system from the esophagus to the rectum have a similar structure and are composed of the same three layers:

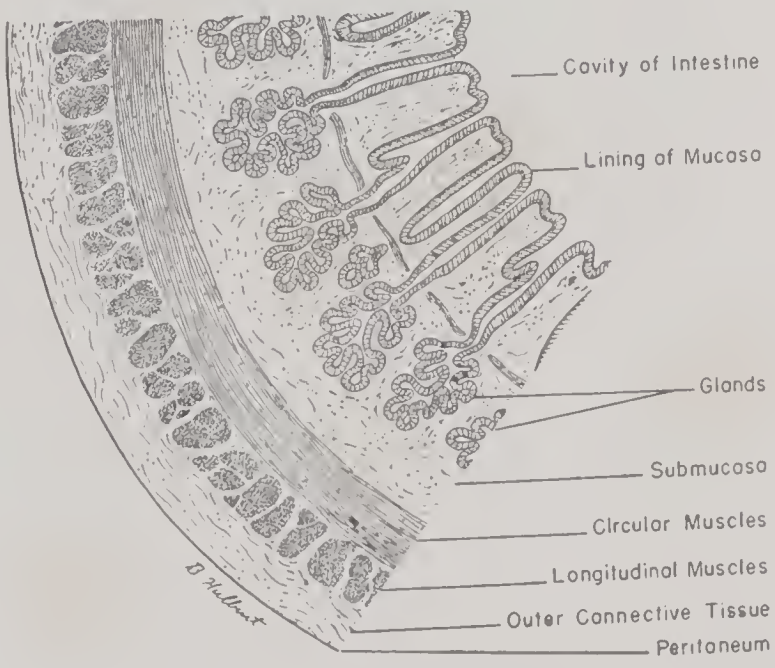


Fig. 97. Cross section of the human intestine.

an inner mucous membrane or mucosa, a muscular middle layer, and an outer layer of connective tissue (Fig. 97). The inner lining of the mucosa, next to the cavity of the tract, is composed of epithelial cells, usually of columnar type, some of which secrete the viscous lubricating mucus. The mucosa in the stomach and intestines is greatly folded to increase the secreting and absorbing surface of the tube. The glands of the digestive tract are formed as out-pockettings of the mucosal lining.

The muscular layer is composed of smooth muscle except in the upper third of the esophagus, where there is striated muscle. Most of the digestive tract has two distinct layers of muscle: an inner one with the

fibers arranged circularly, and an outer one with the fibers arranged longitudinally. By contracting these layers alternately or in unison, the digestive organs can perform a variety of movements to churn the food and move it along.

The outermost layer of the digestive tract is made of strong, flexible connective tissue fibers covered by a smooth sheet of the peritoneum. This sheet secretes a fluid to lubricate the surface of the stomach and intestines and reduce friction as the parts of the digestive tract move and rub against each other and the abdominal wall. The esophagus, which lies buried in the muscles of the neck and chest, has no peritoneal covering.

The walls of the digestive tract are richly supplied with nerves to coordinate the actions of the various parts, and with blood and lymph vessels to supply the cells with food and oxygen, to drain away wastes and to carry the absorbed food to a place of storage.

III. THE PHARYNX

Food passes from the mouth cavity into the pharynx, the cavity behind the soft palate where the digestive and respiratory passages cross.

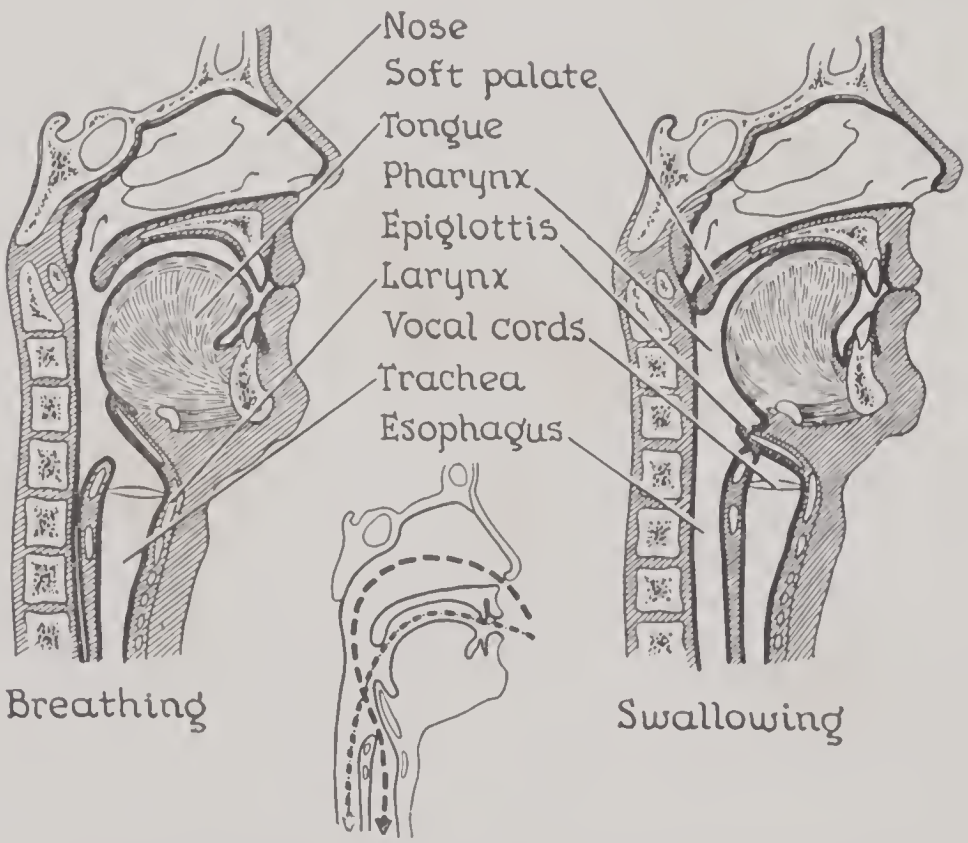


Fig. 98. Diagram of the changes in the position of the tongue, epiglottis and other structures in breathing and swallowing. (Reproduced by permission from The Body Functions, by R. W. Gerard, published by John Wiley & Sons, Inc.)

It has no less than seven tubes connecting with it: the two internal nares from the nasal cavity, the connection from the mouth, the glottis opening into the trachea, the esophagus going to the stomach, and two Eustachian tubes going to the middle ear cavity to equalize pressure on the two sides of the ear drum (see p. 301). An automatic mechanism keeps the substances conducted by these tubes in their proper channels.

4. Swallowing. When the food is ready to be swallowed, a complicated series of reflexes moves it from the mouth to the stomach. The first part of the swallowing act is under voluntary control: the tongue is raised against the roof of the mouth, and the bolus of food between the tongue and palate is pushed into the pharynx by a wavelike movement of the tongue. When swallowing begins, respiration is stopped momentarily by a reflex mechanism to prevent the passage of food into the larynx or trachea. Once the food is in the pharynx, there are four possible exits for it, only one of which is desirable. Normally, the reflex closing of the other three, forces the food down the esophagus when the pharynx contracts. The opening to the nasal cavity is closed by the reflex elevation of the soft palate (Fig. 98), while the tongue is held against the roof of the mouth, preventing the food from returning. The opening into the larynx is closed by the contraction of muscles which raise the entire larynx, bringing the opening, the glottis, under the fold of tissue called the epiglottis. This action completely closes it and prevents food from going down the trachea, and at the same time enlarges the opening of the esophagus to facilitate the passage of the bolus. The raising of the larynx can be observed in the bobbing up of the "Adam's apple" (which is simply the outside of the larynx) each time one swallows.

IV. THE ESOPHAGUS

The esophagus, or gullet, into which food passes next, is a muscular tube leading directly downwards from the pharynx to the stomach. It passes between the lungs and behind the heart, penetrating the diaphragm to reach the stomach. It has well-developed muscular walls: the upper third contains striated muscle; the lower two-thirds, smooth muscle.

The contraction of the muscles in the wall of the pharynx and the presence of the bolus in the upper part of the esophagus cause a single, powerful, rhythmic wave of muscle contraction in the wall of the esophagus, called **peristalsis,** which pushes the bolus down to the stomach. This wave is preceded by one of relaxation which dilates the tube to make room for the food. Similar peristaltic waves move the contents through all the organs of the digestive tube. The wave of contractions is rapid in the esophagus, and it takes only about six seconds for solid food to reach the stomach from the mouth. Liquids are swallowed even faster, since they simply flow downward under the force of gravity. If some of the food escapes the first wave of contraction and remains in the esophagus, it stimulates another muscular contraction to move it to the stomach. An emotional upset, excessive smoking, or food swallowed too hastily may cause the muscles of the esophagus to contract in a spasm when no food is present, resulting in the sensation of a "lump in the throat."

The opening from the esophagus to the stomach is controlled by a ring of smooth muscle, called a **sphincter.** Normally, this is closed; it opens reflexly only when a wave of contraction in the esophagus has pushed a bolus of food against it. As liquids are swallowed, they fall through the esophagus to the sphincter faster than the accompanying

wave of contraction of the esophagus muscles, but the ring of muscle does not open until the peristaltic wave reaches it. Similar sphincters control the movement of food at three other places in the digestive tract: the opening of the stomach into the small intestine, the opening of the small intestine into the large intestine, and the opening at the anus where the digestive tract ends.

V. THE STOMACH

When the food leaves the esophagus, it enters the stomach, a thick-walled, muscular sac on the left side of the body just beneath the lower ribs. This organ is divided into three main regions (Fig. 99): an upper

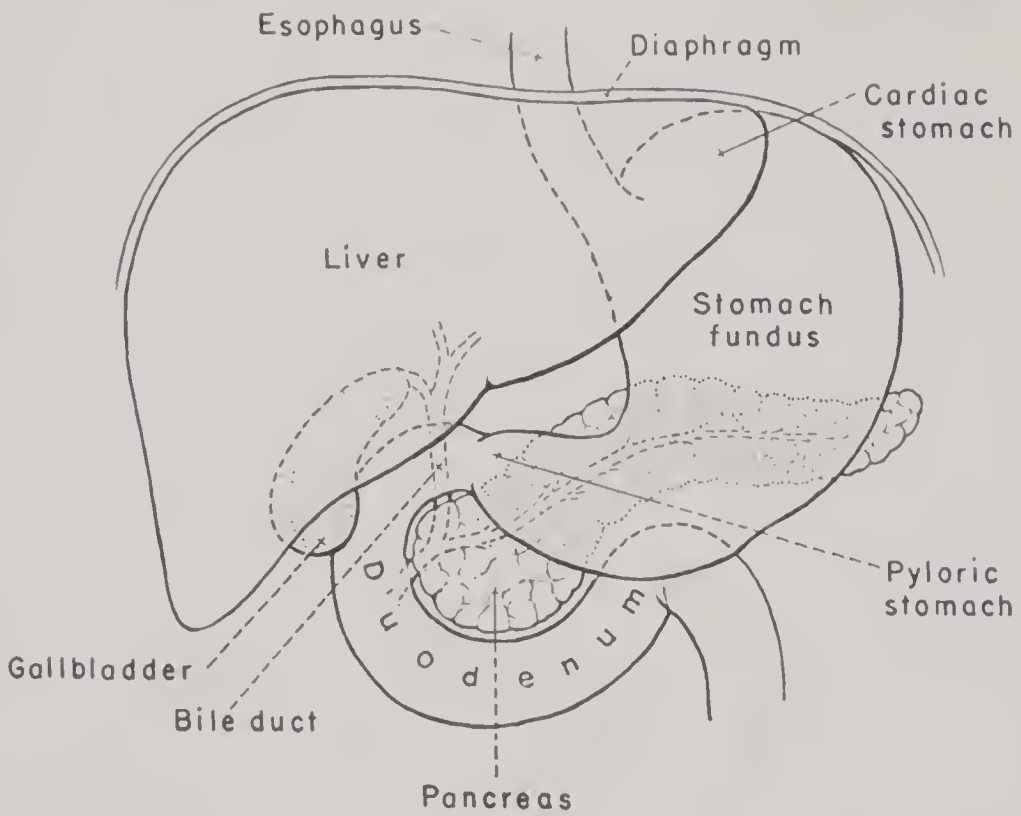


Fig. 99. Diagram of the relations of the stomach, liver, pancreas and duodenum.

part, nearest the heart, called the **cardiac region;** a deep part, below this, called the **fundus;** and an area extending to the opening of the small intestine, called the **pyloric region.** The muscular layers of the stomach wall are exceptionally thick, being composed of a diagonal layer of fibers in addition to the circular and longitudinal fibers found elsewhere in the digestive tract. The mucosa, or lining, of the stomach contains millions of microscopic gastric glands which secrete the gastric juice containing enzymes and hydrochloric acid. Pure gastric juice is extraordinarily acid, having a *p*H of about 1, but the stomach contents, in which the gastric juice is mixed with food, are less acid, with a *p*H of about 3.

The size of the stomach varies, of course, as a meal is eaten and digested. The maximum capacity of the average person's stomach is about 2½ quarts. As swallowing occurs, the stomach relaxes reflexly to make room for the food. Soon after the food reaches the stomach, peristaltic waves begin in the pyloric region, passing from left to right, toward the opening into the intestine. The rest of the stomach, contain-

ing most of the food, remains quiescent at this stage. As digestion proceeds, the waves originate farther and farther to the left, and finally the entire stomach wall, from cardiac to pyloric end, is swept by deep, powerful peristaltic waves which mix the contents and mechanically break the larger bits of food into smaller ones. The food is now the consistency of cream soup, and digestion is well advanced. At intervals, the pyloric sphincter relaxes, and a small amount of **chyme** (as the contents of the stomach and small intestine are called) is pushed into the small intestine by the contraction of the stomach. The opening of the pyloric sphincter at the proper time is regulated by a mechanism whose action is not completely known. The strength of the peristaltic waves in the stomach and the consistency of chyme are important factors in this regulation. In one to four hours, depending upon the amount and kind of food eaten, the stomach is emptied. Carbohydrate foods leave the stomach more rapidly than proteins, and proteins more rapidly than fats. When the stomach is empty it continues to contract, and it is this squeezing of the empty stomach which stimulates nerves in the wall, causing hunger pangs.

5. Vomiting. Occasionally something may be taken into the stomach which should be ejected. To make this possible, most mammals—with the exception of rabbits, rats and other rodents—have a mechanism in the stomach called the vomiting reflex. Vomiting may be caused by mechanical irritation of the pharynx (sticking a finger in the throat is used to induce it when some poisonous substance has been swallowed) or by disturbances in the semicircular canals of the ears, as in seasickness. It is controlled by a center in the midbrain, known as the vomiting center, which coordinates the contraction of the stomach and of the muscles of the abdominal wall, the closing of the pyloric sphincter, the opening of the cardiac sphincter and the closing of the glottis.

VI. THE SMALL INTESTINE

The small intestine, into which the chyme passes by the force of the peristaltic waves in the stomach, is a long coiled tube, about 22 feet long and approximately 1 inch in diameter. This great length is necessary for absorbing sufficient food to maintain life. The greater part of digestion and almost all absorption occur in this organ. Only alcohol and a few poisons can be absorbed through the stomach wall.

The length of the intestine is correlated with the type of diet: plant-eating animals have a long small intestine; meat-eating animals have a short one; and omnivorous ones, like man, have one of intermediate length. An interesting example of this is to be seen in the frog: the frog larva or tadpole is herbivorous and has a long small intestine, but the adult frog is carnivorous and has a much shorter, small intestine.

The first segment of the small intestine, about 10 inches long, is called the **duodenum.** It occupies a fixed position in the abdominal cavity because it is held in place by ligaments connecting it to the liver and stomach, as well as to the dorsal body wall. The rest of the small intestine (and most of the large intestine) is attached only to the dorsal body wall by a thin, transparent membrane called the mesentery, and so is able to move about with considerable freedom. The supporting

mesentery provides a means for nerves and blood vessels to pass from the body wall to the intestine. In the duodenum two extremely important juices reach the digesting food: bile from the liver, and pancreatic juice from the pancreas. In addition, the wall of the intestine contains millions of tiny, intestinal glands which secrete the intestinal juice containing a number of enzymes. These three juices are mixed in the small

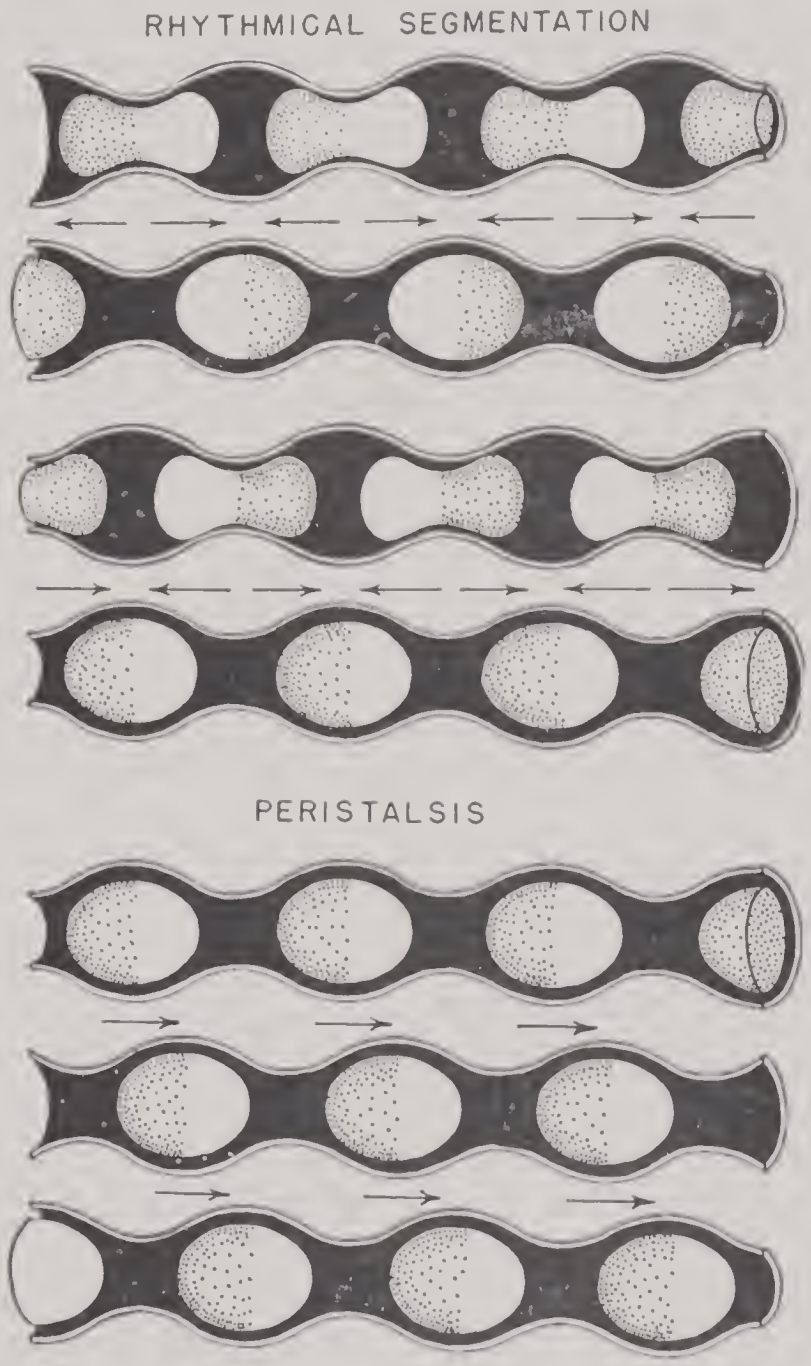


Fig. 100. Diagrams to illustrate the churning action of rhythmical segmentation in the intestine, and the movement of food through the digestive tract by peristalsis. (Hunter and Hunter: College Zoology.)

intestine and complete the digestive process begun in the mouth and stomach.

6. Intestinal Movements. When food is present, the small intestine is more or less constantly in motion, and this intestinal motility is independent of any stimulation from outside, since it continues in laboratory experiments after all the nerves to the intestine are cut. There are two types of intestinal movements, the peristaltic contractions, which move

the chyme along, and the churning movements, which simply mix the intestinal contents (Fig. 100). A single peristaltic wave does not move far in the intestine; usually after 4 or 5 inches it is dissipated, though occasionally, rapid movements, called peristaltic rushes, sweep along for considerable distances. The churning movements are caused by alternating contractions and relaxations of successive segments of the intestine, which are repeated about ten times a minute. These movements complete the mechanical breaking up of the intestinal contents, mix them with the various digestive juices, and ensure that all parts of the intestinal contents will be brought in contact with the intestinal wall so that the digested food may be absorbed into the blood stream. In each part of the intestine these churning movements continue for a time; then a peristaltic wave carries the contents to the next section, and the churning movements begin again. In this way the contents are ultimately carried through the small intestine to the large intestine in about eight hours. By the time the remains of the food pass from the small intestine, digestion has been completed and the digested food particles have been absorbed. The materials passing into the next section of the digestive tract, the large intestine, consist of indigestible matter and large quantities of water derived from the food taken in or from the digestive juices.

VII. THE LIVER

Because of its contribution of the digestive juice, bile, the liver is vitally important to digestion. It is the largest gland in the body, occupying the whole upper part of the abdominal cavity, just below the diaphragm. The greater part of it lies on the right side of the body, but it extends to the left side and partly covers the stomach.

Bile is formed in all parts of the liver and is collected by a branching system of fine ducts, leading into large ducts, which empty into the gall-bladder (Fig. 99), where the bile is stored until needed. Here, water and salts are removed from the bile, so that it may be greatly concentrated. Bile is secreted by the liver cells constantly, but passes to the duodenum only after food has been eaten. Its passage down the common bile duct is brought about by the contraction of the muscular wall of the gall-bladder. Being alkaline, it helps to neutralize the acid chyme.

Since bile contains no digestive enzymes, its chief importance in digestion lies in the action of the **bile salts**. These substances act as emulsifying agents so that when the churning movements of the intestine are going on, a fine emulsion, or suspension, of fat droplets within the chyme is produced. As the fat is broken into small droplets, a greater surface area is created in which the fat-splitting enzyme, lipase, may work; consequently an increase in the speed of the digestion of fat occurs. When bile salts are absent from the intestine, as when the bile duct is obstructed, the absorption as well as the digestion of fats is impaired, and much of the fat eaten is lost in the feces. The bile salts themselves are carefully conserved by the body, being reabsorbed from the lower part of the intestine and carried back to the liver to be secreted over again. Another constituent of the bile, cholesterol, plays no part in digestion, but may cause trouble. Cholesterol is not very soluble

in water, and under certain circumstances the cholesterol in the gall-bladder may be concentrated, by the removal of water, to the point of precipitation, producing the hard little pellets called "gallstones." These may obstruct the bile duct and stop the flow of bile.

The color of bile depends on its pigments. There are two main pigments, a red one and a green one, which are present in different proportions in different vertebrates, so that the color of bile ranges between them; human bile is a deep yellow-orange. In the intestine the bile pigments undergo chemical alterations which change them to a dark brown, and it is to these pigments that the brown color of the feces is due. When the bile is obstructed so that bile pigments are not present in the feces, the latter are whitish or clay-colored. In such a condition, and in certain impairments of the functioning of the liver, the bile pigments accumulate in the blood and tissues, giving a yellowish tinge to the skin, a condition known as jaundice.

VIII. THE PANCREAS

At the same time that the food in the duodenum is acted upon by the bile, it is also mixed with a juice from the other main digestive gland, the pancreas. This gland is an irregular, diffuse mass lying between the stomach and the duodenum (Fig. 99). Its secretion, the pancreatic juice, containing a number of enzymes, passes into the duodenum by way of the pancreatic duct. In addition, certain cells of the pancreas, called the islets of Langerhans, secrete into the blood stream the hormone insulin (p. 316). These two secretions are entirely separate and unrelated. It just happens that in man, and most vertebrates, the two types of cells occur together in the same gland; in certain types of fish the two types are spatially separated into two different glands.

The pancreatic juice is a clear, watery fluid that is quite alkaline, with a *p*H of about 8.5. It is the main factor in neutralizing the acid chyme. The enzymes secreted by the pancreas and the intestinal wall will not work in an acid medium; hence the need for a neutralizing agent after food has been received from the stomach. Experiments indicate that an average person secretes about 1 or 1.5 liters of pancreatic juice each day. If the pancreatic duct becomes blocked so that the pancreatic enzymes are unable to reach the intestine and act on the food, the person develops a tremendous appetite and eats a great deal. In spite of this he loses weight, which demonstrates the importance of the pancreatic juice in normal digestion.

IX. THE ABSORPTION OF FOOD

After food has been digested, it must be absorbed into the body through the lining of the digestive tract. Most of the absorption is done by the small intestine, particularly the lower part of this organ. Water is absorbed by the colon, but almost all organic and inorganic substances are absorbed through the small intestine. The greater the surface of the small intestine, the greater is its ability to absorb foods. To increase the rate of absorption, the lining of the small intestine is greatly folded. In addition, countless small finger-like projections called **villi**, each of

which contains a network of blood capillaries and a lymph capillary in its center, cover the inner surface of these folds (Fig. 101).

Absorption is a complex process, involving in part the simple diffusion of substances from the cavity of the intestine through the lining cells and into the blood or lymph capillaries. This may take place even when there is a greater concentration of the substance in the blood stream than in the intestine. In such circumstances the cells lining the intestine must do work and "pump" these substances into the blood stream against the diffusion gradient, a process analogous to secretion.

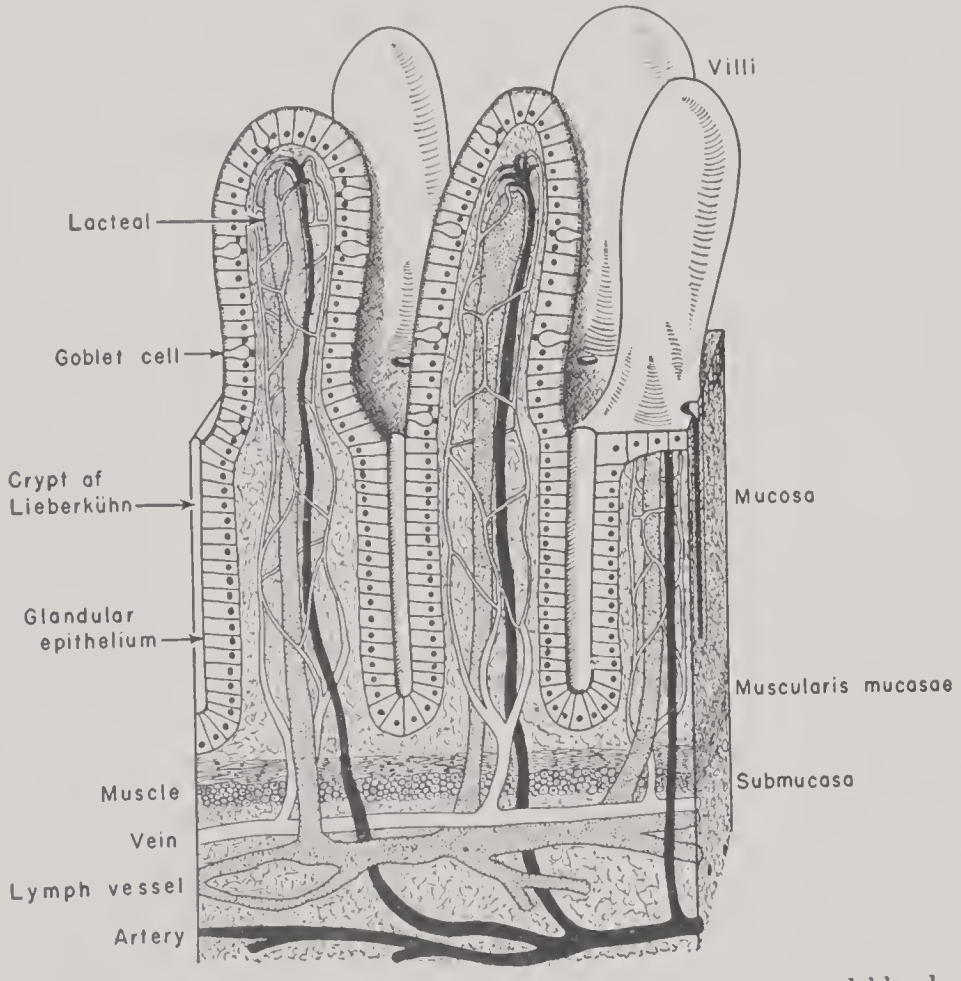


Fig. 101. Detailed diagram of intestinal villi, showing their structure and blood and lymph supply. (Hunter and Hunter: College Zoology.)

in which cells do work to move substances from one region to another. The cells lining the intestine constitute a semipermeable membrane and as such permit certain substances, such as amino acids and glucose, to pass through while preventing the passage of others, such as intact protein and starch molecules. Glucose and amino acids are absorbed into the blood capillaries and carried by the hepatic portal vein to the liver for storage, later to be distributed to the rest of the body. We shall return to the importance of the liver in storing these substances, changing them into others, and maintaining a relatively constant level of them in the blood (p. 218).

The absorption of glycerol and fatty acids is by quite a different route. As these substances pass through the mucosal cells of the villus, they are resynthesized into molecules of fat. These combine into fine globules

which are too large to pass through the capillary walls into the blood stream and pass instead to the lymph vessel. During the absorption of a meal rich in fat the lymphatic vessels of the intestine have a milky white color due to this fat emulsion. These intestinal lymph vessels eventually empty into the great thoracic duct and from there into the blood stream, since the great thoracic duct empties into the left shoulder vein. The fat eventually gets into the blood stream and is distributed to the body, but its route is less direct than that of the sugars and amino acids.

X. THE LARGE INTESTINE AND RECTUM

From the small intestine, what is left of the food after absorption passes into the large intestine, or **colon**, a U-shaped tube, larger in diameter and with thicker walls than the small intestine. It consists of three parts, the ascending, transverse, and descending colons (Fig. 94) The small intestine does not connect with the end of the large intestine, but empties into its side, a short distance from the extreme end in the lower right corner of the body near the hip bone. This arrangement leaves a large blind sac, called the cecum, at the tip of which is a small projection about the size of the little finger, the appendix. The cecum and appendix were larger in our remote ancestors and active in the digestion of vegetable materials. Herbivores such as rabbits and guinea pigs still have a large functional cecum. As we evolved and changed our food habits, the cecum became superfluous and degenerated. From the junction of the small and large intestines, the ascending colon runs up the right side of the body to the level of the liver. The colon then makes a right-angle turn and, as the transverse colon, runs across the abdominal cavity just below the liver and stomach. When it reaches the left side of the body it makes another right turn, becomes the descending colon, and passes down the left side of the body to the rectum.

The material reaching the colon from the small intestine has had most of the nutrients absorbed from it, but it is still liquid, because, although some water is absorbed in the small intestine, almost as much water is added by the bile and pancreatic juice. The main function of the colon, in addition to transporting the wastes to the rectum to be ejected from the body, is to absorb water and reduce the wastes to a semisolid state. The same two movements occur in the colon as in the small intestine—churning and peristaltic—although both are ordinarily slower and more sluggish than those in the small intestine. Periodically, more vigorous peristaltic movements force the contents along, until they finally reach the rectum. These occur especially after eating, because of a reflex mechanism whereby the filling of the stomach stimulates an emptying of the colon. This mechanism, called the gastrocolic reflex, is responsible for defecation usually occurring after a meal.

Defecation is partly voluntary, depending upon the contraction of the abdominal wall muscles and the diaphragm, and the relaxation of the outer ring of muscle (sphincter) of the anus, and partly involuntary, depending on the relaxation of the inner anal sphincter and the contraction of the large intestine and rectum which forces the feces out

through the anus. It is the distention of the rectum and the consequent stimulation of nerves in its walls that bring about the desire to defecate. If this signal is ignored, the rectum adapts to the new size and the stimulus diminishes and finally disappears.

It takes from twelve to twenty-four hours for the waste products of digestion to pass through the colon and rectum. The end product, the feces, contains indigestible remnants of the food, certain substances secreted by the body, such as bile pigments and heavy metals, and large quantities of bacteria. The latter make up about half of the mass of the feces.

The entire digestive tract, and especially the colon, contains great numbers of these bacteria, which do no harm, and may even be useful. For instance, the cellulose walls of plant cells are not broken down by the enzymes of most animals, but are affected by enzymes from the bacteria. In herbivores the large cecum provides a place for such material to be kept while the action of the bacteria takes place. Another function of the bacteria is to synthesize a number of the vitamins, and an appreciable amount of certain ones are manufactured by the intestinal bacteria and absorbed through the colon. Some bacteria in the colon produce substances highly poisonous and odorous, and at one time it was thought that the absorption of them, especially in constipation, might be dangerous, but more recent studies show that they are never present in dangerous amounts in the general blood stream, because of the detoxifying action of the liver.

The headaches and other symptoms which usually accompany constipation are not caused by absorption of "toxic substances" from the feces at all, but are due to the distention of the rectum. If the rectum is packed with some inert substance such as cotton, the same symptoms appear.

If the lining of the colon is irritated, as in an infection such as dysentery, peristalsis is increased and the intestinal contents are passed through rapidly, with only a small amount of the water removed from them. This condition, known as **diarrhea**, results in frequency of defecation and, of course, watery feces. The opposite condition, **constipation**, results when the contents pass through too slowly, so that an abnormally large amount of water is removed, and the feces become excessively hard and dry. Modern civilization, and the sedentary life and nervous strain which it produces, tend to decrease intestinal motility and may cause constipation. People often become unduly alarmed when a day or two passes without a bowel movement (the constant exhortations of the vendors of laxatives in the press and on the air have something to do with this!), and usually take something to induce defecation. In most cases nothing is wrong, and the taking of cathartics and laxatives does more harm than good. The repeated use of these preparations, because of their irritating effect on the colon, leads to a condition known as cathartic constipation, in which the muscles in the colon become incapable of their normal churning and peristaltic movements and remain contracted. Constipation can be avoided by eating foods that contain sufficient indigestible cellulose fibers ("roughage") to give bulk to the intestinal contents.

XI. DISORDERS OF THE DIGESTIVE TRACT

We have already discussed certain disorders of the digestive system—gallstones, diarrhea and constipation. Another common complaint is "indigestion," which may result from overeating, from the irritation of the stomach lining by an excess of alcohol, or from some disturbance in the functioning of the colon. Since the transverse colon lies just beneath the stomach, it is sometimes difficult to distinguish the source of pain. Any constantly recurring indigestion should receive medical attention. Constant nervous strain may impair the functioning of the digestive system and produce indigestion. Whenever you hear or read an advertisement for some remedy for "acid stomach," remember that the stomach is *normally* acid, and must be acid for pepsin to act, and to stimulate the secretion of secretin, which causes the pancreas to give off pancreatic juice.

About one person in a hundred has a stomach **ulcer,** an area in the stomach where the lining is eroded. The cause of ulcer formation is not clear, but may depend on the secretion of an unusually acid gastric juice, mechanical injury of the wall by some sharp object, or by some interference with the blood supply to the cells lining the stomach so that they are unable to secrete enough protecting mucus. The pain associated with an ulcer is believed to be caused by the contact of the acid gastric juice with the eroded surface, and the danger lies in the fact that the erosion of the wall may increase and reach a large blood vessel, resulting in hemorrhage and death; or the wall may be eroded all the way through so that the stomach contents, which contain bacteria, pass into the peritoneal cavity, causing general inflammation of the peritoneum (peritonitis).

One of the weak spots of the digestive tract is the appendix. The cause of the inflammation of this organ (appendicitis) is not known, but again, the danger lies in the possible rupturing of its wall and the release of bacteria into the peritoneal cavity, which may cause peritonitis and death. The surgical removal of the inflamed organ before it bursts is an effective cure.

XII. THE CHEMISTRY OF DIGESTION

The chemical reactions which result in the breakdown of food molecules to simple substances which can be absorbed through the intestinal wall are regulated by **enzymes;** these, you will remember, are organic catalysts which enable the body to bring about chemical reactions that can be duplicated in the test tube only at high temperatures and pressures, if at all. Enzymes are *specific;* each will catalyze a certain reaction and no other. For example, a protein-splitting enzyme has no effect on a molecule of fat. The chemistry of digestion is best understood by studying the enzymes involved (Table 6). The names of most enzymes are a combination of *-ase* with the name of the substance worked upon. Thus, lipase means the enzyme acting on fats (lipids). Some of the enzymes, discovered in early days before this convention was agreed upon, have names ending in *-in.* An attempt was made at one time to change all the old names to ones ending in *-ase,* but it was unsuccessful.

7. Saliva. The first enzyme encountered by food in the digestive tract is **ptyalin,** present in the saliva. Ptyalin attacks cooked starch and other complex carbohydrates by hydrolyzing or splitting them into double sugars, principally maltose, the malt sugar of "malted milk." Although this chemical splitting of starches by ptyalin occurs fairly rapidly, it cannot be completed while the food is in the mouth in the normal time required for chewing. Most of the splitting occurs within each bolus of food in the stomach before the gastric juice penetrates and renders the food too acid for ptyalin to work. Different people have saliva containing different amounts of ptyalin, so that the time required to digest a given amount of starch varies. You can test the activity of your own

Table 6. Enzymes Important in Digestion

Location	Enzyme	Source	Optimum *p*H	Substance Acted Upon	Product
Mouth	Ptyalin	Salivary glands	Alkaline	Cooked starch	Double sugars
Stomach	Pepsin	Gastric glands	Acid	Proteins	Proteoses and peptones
Stomach	Rennin	Gastric glands	Acid	Milk proteins	Denatured (curdled) protein
Small intestine	Trypsin	Pancreas	Alkaline	Proteins or peptones	Peptones and amino acids
Small intestine	Lipase	Pancreas	Alkaline	Fats	Fatty acids and glycerol
Small intestine	Diastase	Pancreas	Alkaline	Intact or partly digested starch	Double sugars
Small intestine	Erepsin	Intestinal glands	Alkaline	Peptones	Amino acids
Small intestine	Maltase	Intestinal glands	Alkaline	Maltose (double sugar)	Glucose (simple sugar)
Small intestine	Sucrase	Intestinal glands	Alkaline	Sucrose	Simple sugars
Small intestine	Lactase	Intestinal glands	Alkaline	Lactose (milk sugar)	Simple sugars
Small intestine	Enterokinase	Intestinal glands	Alkaline	Trypsinogen (inactive)	Trypsin (active)

saliva by a simple experiment based on the fact that starch plus iodine is blue, while sugar plus iodine is not. Put 10 cc. of a dilute boiled starch solution in a test tube and add 1 cc. of saliva. Mix thoroughly and at the end of each minute after adding the saliva, remove a drop and add it to a drop of iodine solution. At first the solution will be blue; later samples will be violet or red, and finally the samples will be colorless, indicating that the starch has been digested to maltose. The red color is due to the intermediate substances formed in the breakdown of starch to sugar. Because ptyalin, and all enzymes, are proteins and "denatured" (changed by heating), so that they no longer function, you can prove this to be an enzyme-controlled reaction by repeating the test, using saliva that has been boiled. Saliva also contains some maltase, which breaks maltose down to form glucose.

8. Gastric Juice. The second enzyme to act on the food in its passage through the digestive tract is **pepsin,** secreted by certain cells of the

gastric glands in the fundus of the stomach. Other cells in the fundus secrete hydrochloric acid. The glands in the pyloric regions secrete mucus, and the entire lining of the stomach contains other mucus-secreting cells.

Pepsin splits the large molecules of protein into smaller, soluble molecules known as proteoses and peptones, but is unable to complete the breakdown of these to their constituent amino acids. This is done by other enzymes in the intestine. Pepsin is active only in an acid medium and any acid will speed up its action, but hydrochloric acid is most effective. In contrast, the protein-splitters of the intestine, trypsin and erepsin, operate only in an alkaline medium. All the body cells have intracellular protein-splitting enzymes (called cathepsins) which act in an essentially neutral medium.* If a piece of tissue is removed from the body and kept moist and warm, the cathepsins in it will eventually dissolve it. Pepsin is secreted by the gastric glands in an inactive form, called pepsinogen; this is converted into pepsin when it comes in contact with acid.

Gastric juice also contains an enzyme known as **rennin,** which acts on a specific protein present in milk, casein, changing it from a soluble to an insoluble form, thereby curdling the milk. This is necessary to keep milk in the stomach long enough for pepsin to act upon it, since, if milk remained liquid, it would pass through as rapidly as water. For centuries rennin has been extracted from the stomachs of calves and used in making certain types of cheese, and the milk pudding "junket" is made with rennin.

Since the stomach wall is made of protein, you may wonder why it is not digested by the pepsin and hydrochloric acid it secretes. The stomach has a number of safeguards against this, but when they fail, the wall is digested and an ulcer results. The entire stomach wall is normally lined with a thick coat of mucus which protects it from the active enzyme. This coat is constantly renewed by the mucus-secreting cells lining the stomach. When the stomach is empty, little gastric juice is secreted, and that present has a low acidity, so that the pepsin is not very active. At the end of a meal, a little of the alkaline intestinal juice passes through the pylorus into the stomach and neutralizes the acid there. All these factors serve to protect the lining of the stomach from the action of pepsin.

9. Pancreatic Juice. In the small intestine the enzymes of the pancreatic juice continue the digestion of carbohydrates and proteins begun by the saliva and gastric juice and perform almost all the digestion of fats. The three main enzymes secreted by the pancreas are **trypsin, diastase** and **lipase.** Trypsin acts on intact or partially digested protein molecules, breaking them up into simple groups of several amino acids. Since trypsin can digest intact proteins, some mechanism is necessary to protect the pancreas itself from digestion. This enzyme is not secreted in an active form, but as an inactive substance called trypsinogen.

* Plant cells also have protein-splitting enzymes, which may be present in large quantities. For example, pineapple contains so much protein-splitting enzyme that one cannot prepare a gelatin containing fresh pineapple. After pineapple has been heated, as in canning, the enzyme is destroyed, so that canned pineapple can be used in gelatin salads.

The trypsinogen passes down the panereatie duct and is aeted upon in the intestine by another enzyme, **enterokinase,** secreted by glands in the wall of the intestine, whieh converts it into aetive trypsin. If active trypsin does get into the pancreas aceidentally, it will digest it and eause death. The second pancreatic enzyme, diastase, supplements the aetion of ptyalin and digests cooked or uncooked starehes to maltose. It is more important than ptyalin in the digestion of starehes and has a longer time to work on them. Most animals do not have ptyalin in their saliva, but rely on pancreatic diastase to digest the starehes eaten. Lipase, the third pancreatic enzyme, breaks moleeules of fat into one moleeule of glyeerol and three molecules of fatty aeids; the latter ean be absorbed by the intestinal walls, but fat cannot. Since the pancreas is the only gland scereting appreciable amounts of a fat-splitting enzyme, there are more marked disturbances in fat digestion than in protein or earbohydrate digestion when the flow of the panereatic juiee is interfered with. In such cases, fat passes through the digestive traet essentially unchanged and is lost in the feces.

10. Intestinal Juice. The walls of the intestine eontain a large number of small glands whieh secrete additional enzymes to eomplete the digestion of proteins and earbohydrates. It is diffieult to measure the amount of intestinal juice secreted, but it is estimated to be about 3 liters daily. The enzyme **erepsin** completes protein digestion, splitting small groups of amino acids into individual ones whieh ean be absorbed. **Maltase, sucrase** and **lactase** are enzymes that aet on malt sugar, eane or beet sugar and milk sugar to split them into simple sugars sueh as glucose. The intestinal glands secrete enterokinase, the agent whieh transforms trypsinogen into trypsin. The intestinal walls also secrete large amounts of mucus to lubricate the passage of food.

By the time the chyme reaehes the lower part of the small intestine, digestion is complete and absorption oeeurs rapidly; the proteins have been split into their component amino aeids, earbohydrates into simple sugars, and fats into glycerol and fatty aeids.

In addition to the enzymes secreted by the digestive traet, other digestive enzymes are secrcted by baeteria in the eolon. In man and the carnivores baeterial enzymes are not very important, but the eellulose-digesting enzymes seereted by bacteria are vital to herbivorous animals. Termites afford an extreme example of the dependenee of one organism on another for a digestive enzyme. These animals are voraeious wood caters, yet they have no enzymes for digesting it. In their intestines, however, live eertain flagellate protozoa that ean digest wood (eellulose) to sugars. Although the flagellates use some of this sugar as a souree of their own energy, there is enough left over for the termite. Termites could not survive without their intestinal inhabitants, and newly hatched termites instinetively liek the anus of another termite to obtain a supply of flagellates. The flagellates also benefit by this arrangement: they are supplied with plenty of food and the proper environment; in faet they can survive only in the intestines of termites. Sueh an arrangement, where two organisms live together in a elose relationship to their mutual benefit, is ealled **mutualism** or symbiosis (see p. 102).

XIII. METHODS OF STIMULATING THE DIGESTIVE GLANDS

Each of the glands secreting enzymes must be stimulated to give off its product at the proper time. It would be wasteful and even harmful if the glands secreted constantly. The coordination of the flow of the digestive juices with the presence of food is achieved in two ways—by the brain and by hormones. Hormones are chemical substances secreted in one part of the body and carried by the blood stream to another part where they produce a specific effect.

The salivary glands are controlled entirely by the nervous system. Either smelling or tasting food stimulates nerve cells in the nose or mouth to send impulses to the salivation center in the medulla of the brain; these are relayed to the salivary glands, causing them to secrete saliva. The mere mechanical presence in the mouth of tasteless, odorless objects, such as pebbles, stimulates other cells in the lining of the mouth which act similarly to cause salivation. Or impulses may come from the higher centers of the brain—simply seeing or thinking of food can bring about salivation. The salivary glands will respond, then, to chemical, mechanical or psychic stimuli. It is necessary to have the flow of saliva under rapid nervous control, since the food remains in the mouth such a short time.

Much of our knowledge of the mechanism controlling the secretion of gastric juice we owe to the Russian physiologist, Pavlov, who devised many experimental techniques (such as the Pavlov pouch) and performed many critical experiments. One of these was to sever the esophagus of a dog bringing the two cut ends to the surface of the neck so that when the dog was fed, the food, instead of going to the stomach, went out through the hole in the neck. Although the food was not used, such a "sham-feeding" caused a flow of gastric juice, about one quarter of the normal amount (the normal amount of gastric juice in man is 400 to 800 cc. per meal). This quarter of the normal flow is stimulated by nerve impulses originating in the taste buds, or in the eye, and passing to the brain, whence they go to the stomach. The flow is completely abolished when the nerves to the stomach are cut. By putting food into the cut end of the esophagus leading to the stomach, and preventing the dog from seeing, smelling or tasting it, about half the normal flow would be stimulated when the food reached the stomach. This flow occurs even when the nerves to the stomach are cut, although in reduced amount. It therefore depends in part on nervous stimulation of the gastric glands by impulses from cells in the stomach lining, and in part on a hormone called **gastrin.**

Gastrin is formed by the cells of the mucosal layer of the pyloric part of the stomach and is discharged into the blood stream whenever partly digested food comes into contact with these cells. If extracts of the cells are injected into an animal, the gastric glands begin to secrete within a short time. The final proof of the existence and action of this hormone was given by cross circulation experiments, in which the blood system of one dog was connected by rubber tubes with that of another. When food was placed in the pyloric region of one dog, the gastric glands of the other began to secrete. Since there were no nerve connections between the two dogs, the secretion of gastric juice by the second dog must

have been caused by the substance carried by the blood, the hormone gastrin.

Finally, some secretion of gastric juice is caused by the presence of food in the intestine. Perhaps amino acids, absorbed into the blood from the small intestine, are responsible for this, or it may be caused by some as yet unrecognized reflex or hormone. The operation of so many different mechanisms enables the stomach to provide the proper amount of gastric juice for the type of food eaten. A meal high in protein content causes a copious amount of gastric juice to flow; a meal with little protein and much carbohydrate causes a moderate flow; while one with a high fat content causes a small flow.

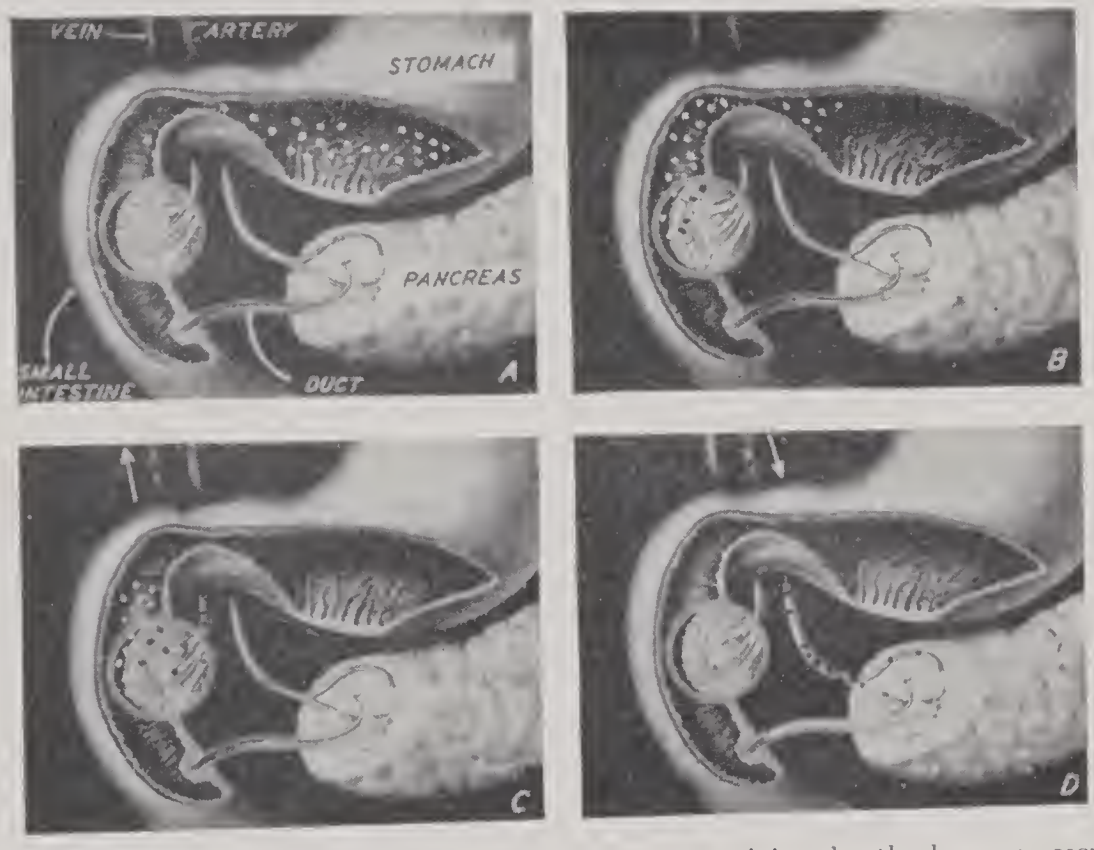


Fig. 102. Control of the release of pancreatic digestive juices by the hormone secretin. *A*, The stomach is shown secreting hydrochloric acid (white dots), which passes to the small intestine. *B*, Some of the hydrochloric acid diffuses into the cells lining the small intestine and stimulates them to form secretin (black dots). *C*, Secretin formation continues, and some of the secretin molecules pass into the vein which is a branch of the hepatic portal vein. *D*, Some of the secretin, after having passed through the heart and lungs, is carried via the pancreatic artery to the pancreas, where it stimulates the cells to secrete pancreatic juice. The juice (shown as white in the pancreatic duct) flows into the small intestine. (From the sound film: Digestion of Foods.)

The stimulation of the pancreas depends upon a hormone, **secretin**, given off by cells in the lining of the upper part of the small intestine. These in turn are stimulated by the acidity of the food entering the intestine from the stomach; they can be stimulated experimentally by introducing acid into the cavity of the small intestine. Normally, as the acid chyme enters the small intestine, it stimulates the cells in the wall to give off secretin into the blood vessels of the intestine. The hormone, carried by the blood stream all over the body, finally reaches the pancreas and causes it to secrete the enzymes it has prepared (Fig. 102). Secretin also causes an increased production of bile by the liver.

When the nerves to the panereas are stimulated, little seeretion results; and when they are eut, there is little or no suppression of the flow, indicating that its seeretions are almost entirely dependent on secretin.

XIV. COMPARISON OF DIGESTIVE SYSTEMS OF OTHER ANIMALS

The ehemistry of digestion and the enzymes involved are mueh the same in man as in the ameba, but the protozoa, whose bodies consist of single eells, do not, of eourse, have any digestive system. Digestion in

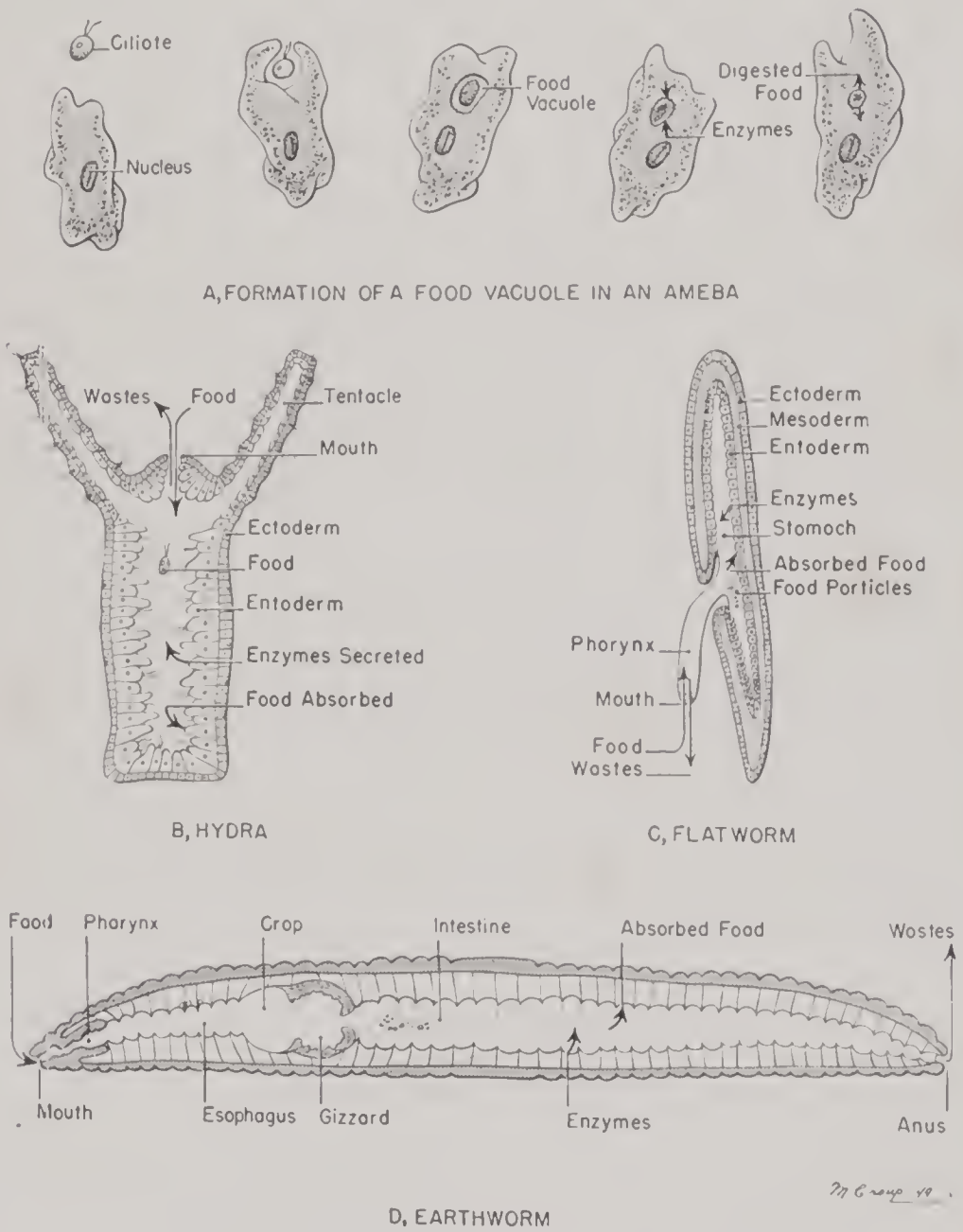


Fig. 103. Digestion in some of the lower animals.

protozoa is intraeellular, oeeurring within the single eell which is the entire animal. An ameba engulfs a bit of food by oozing around it and forming a food vaeuole in whieh the food is shaped into a ball and surrounded by a membrane (Fig. 103). Digestion occurs within this vacuole as it cireulates in the eytoplasm. The digestive enzymes manufactured by the eytoplasm are poured into the vaeuole and digest the food inside. The broken down food molecules are then absorbed through the vacuole wall into the eytoplasm, where they are assimilated or used for energy.

The hydra, although multieellular, has no differentiated organs and

therefore can have no digestive system. The body consists of two layers of cells (Fig. 103), an outer layer of ectoderm for protection and an inner entoderm. Only the cells of the entoderm are capable of digestion. Food, consisting of smaller animals and plants caught by the tentacles, enters the central cavity via the one central opening of the body. The entoderm cells secrete enzymes into this cavity, where the food is broken down into small pieces and then absorbed into the entoderm cells, where digestion is completed. Digestion is, then, partly extracellular, occurring in the space outside the cells, and partly intracellular. There is no anal aperture; undigested wastes are excreted via the opening through which food enters.

In the flatworm, planaria, the digestive organs are the mouth, pharynx and stomach; as in hydra, there is no anus, and food enters, and wastes leave, by the same aperture (Fig. 103). The stomach is greatly branched and extends throughout most of the body, facilitating the distribution of digested and absorbed food. Digestion is both extracellular and intracellular and is carried on by the entoderm cells. These animals have the peculiar ability of digesting their own organs when starved, and so can go for many months without eating. The organs of the body slip, cell by cell, into the cavity of the stomach and are digested.

The next stage in the evolution of the digestive system is demonstrated in the earthworm. This animal has a complete digestive system with two apertures, mouth and anus, so that food travels a one-way traffic road. The system consists of a mouth, a muscular pharynx, which is capable of turning inside out and extending through the mouth to bring food inside, an esophagus, a soft-walled crop where food is stored, a hard, muscular gizzard where it is ground up with the aid of small pebbles taken in with the food, a long straight intestine where extracellular digestion occurs, and an anus through which undigested wastes pass (Fig. 103).

As the higher animals such as the vertebrates evolved, this system was gradually elaborated and organs added, resulting in the complex human mechanism we have just discussed. The digestive system of the vertebrates from fish to man is similar, and in all animals, from lowest to most complex, the chemistry of digestion and the enzymes involved are much alike.

QUESTIONS

1. What are the three functions of the digestive system?
2. Name the organs of the digestive system in order, and state what functions each performs.
3. What keeps the food moving through the digestive system?
4. Why is bile important in digestion? Where is it manufactured, and how does it reach the food?
5. What are gallstones, and how are they formed?
6. What are the islets of Langerhans? What is the relationship of insulin to the pancreatic juice?
7. Discuss how glucose and amino acids are absorbed. How does this process differ from the absorption of glycerol and fatty acids?
8. What are enzymes, and what part do they play in digestion?
9. Name the enzymes of the digestive system and state what foods each one acts upon.
10. What prevents the stomach from being digested by its own secretions?
11. What controls the secretion of the digestive enzymes?
12. Discuss the way digestion occurs in a paramecium, a hydra, a flatworm and an earthworm.
13. Describe the path taken by a molecule of sugar from the mouth to the liver.

SUPPLEMENTARY READINGS

Beaumont, W.: *Experiments and Observations on the Gastric Juice and the Physiology of Digestion.* Cambridge, Harvard University Press, 1929.
The original book by Beaumont, reprinted in 1929, gives an interesting account of his observations on the stomach of Alexis St. Martin.

Best, C. H., and Taylor, N. B.: *The Living Body.* New York, Henry Holt & Company, Inc., 1944.
A clear, understandable presentation of human physiology.

Carlson, A. J., and Johnson, V.: *The Machinery of the Body.* 3rd ed. Chicago, University of Chicago Press.
A well-written and illustrated discussion, on a fairly simple level, of human physiology.

Fulton, J. F.: *Howell's Physiology.* 16th ed. Philadelphia, W. B. Saunders Company, 1949.
One of the standard, detailed, advanced texts of physiology.

Gerard, R. W.: *The Body Functions.* New York, John Wiley & Sons, Inc., 1941.
An interesting account of circulation, digestion and excretion in man.

CHAPTER 12

METABOLISM AND NUTRITION

FOOD may be defined as any substanee taken into the body whieh ean be utilized for the release of energy, for the building and repair of tissues, or for the regulation of body proeesses. This broad elassification includes carbohydrates, fats, proteins, water, mineral salts and vitamins. The first three are energy produeers; the latter three, though not energy produeers, are equally essential to life.

After being taken into the body, foods participate in a variety of chemical reaetions, and these, plus all the other ehemieal activities of the organism, go under the name of **metabolism.** The metabolie process is one of the outstanding eharaeteristies of living things. After foods are absorbed from the intestine they are either built into new tissue or oxidized to provide energy. Some of this energy is used in the building of new tissue, some in the funetioning of the eells (transmission of nerve impulses, contraetion of muscles, secretion of enzymes, and so forth), and some appears as heat. The ehemieal proeesses involved in the building up of substances to make new tissue, or for storage, are referred to as **anabolism.** The opposite term, **catabolism,** refers to ehemieal processes which break down complex substanees to simpler ones, releasing energy. There are many ways of subdividing the general field of metabolism. We may study the metabolism of a single tissue—e.g., liver metabolism—or we may study the ehemical reaetions undergone by a particular kind of food. Carbohydrate metabolism, for example, ineludes all the chemical reaetions which starehes and sugars undergo from the time they are taken in, until, after digestion and absorption, they are stored, eonverted into something else, or oxidized for energy and leave the body as carbon dioxide and water.

Human beings, unlike many other animals, ean adapt to a variety of diets. We are able to operate quite well on one made up chiefly of protein with only small amounts of fats and earbohydrates, on one eomposed mainly of carbohydrate, with small amounts of proteins and fats, or even on one that is primarily fat with small amounts of the others. The diet of Eskimos is an example of the last.

The energy requirements of the body are expressed in terms of the Calorie, which is the amount of heat required to raise 1 kilogram of water 1 degree Centigrade.* Although the body can obtain the greater part of its energy requirements from any of the three types of fuels, they are not equally effective: the oxidation of a gram of carbohydrate or protein in the body yields about 4 Calories, but the oxidation of a gram of fat yields about 9 Calories. That is why such foods as whipped eream, mayonnaise and butter are more fattening than fruits, meat or bread.

* A chocolate cream, containing 100 calories, could, if all its energy were utilized, bring a kilogram of water from the freezing to the boiling point.

In the average American diet about two thirds of the energy used daily comes from carbohydrates and one sixth each from proteins and fats.

I. THE BASAL METABOLIC RATE

The daily expenditure of energy varies widely from person to person, depending on activity, age, sex, weight and body proportions. In order that doctors may make comparisons between the metabolic rates of different people and detect abnormally low or high rates, the conditions under which metabolism is measured must be standardized. If a person is reclining at complete rest, at least twelve hours after his last meal, the energy used from moment to moment keeps the heart beating and the breathing movements going, but most of it is used to maintain the body temperature. The amount of energy expended by the body just to keep alive, when no food is being digested and no muscular work is being done, is called the **basal metabolic rate.** The basal metabolic rate for young adult men is about 1600 Calories per day; for women it is about 5 per cent less. In other words, if a young adult remained in bed for twenty-four hours without eating or moving he would expend about 1600 Calories in keeping alive. By making thousands of determinations of the basal metabolic rate on different people, tables have been established giving the normal basal metabolic rate for a given age, sex and total body area. The rate is proportional to the surface area of the body, which can be calculated from the height and weight. A normal young adult uses 40 Calories per square meter of body surface per hour.

The higher the temperature of the body, the more rapidly chemical reactions occur, the basal metabolic rate increasing about 5 per cent for each degree of rise in temperature. This is the primary reason why weight is lost during feverish illnesses.

The basal metabolic rate can be determined directly by measuring the heat given off. The subject is placed in an insulated chamber surrounded by water, and the increase in the temperature of the air in the chamber and the surrounding water is measured. The simpler, clinical method is to determine the person's oxygen consumption over a short period of time. Since the release of energy and the production of heat depend on the uniting of oxygen with glucose and other foods, the amount of heat produced can be calculated from the amount of oxygen consumed.

1. Energy Requirements. If a person remains in bed for twenty-four hours and receives nourishment, he will expend about 1800 Calories, the extra 200 being required for movements of the muscles of the digestive tract and for secretion of the digestive juices. A person living a sedentary life uses about 2500 Calories per day, the additional 700 supplying energy for contraction of the body muscles and the additional work of the heart, since it beats faster. With heavy physical work, the daily expenditure of energy may reach 6000 Calories.

When the number of Calories taken in as food just balances the energy requirement, the body weight does not change. Most people achieve a balance between the intake and outgo of Calories, and their weight remains remarkably constant for years. There is a tendency for middle-aged people to gain weight because physical activity, but not appetite, decreases with age.

When the caloric intake is less than the daily energy requirement, the body must draw on its stored materials. The first to be used are the carbohydrates, stored as glycogen (sometimes called animal starch) in the liver and muscles. These are exhausted within twenty-four hours. Next, fat is withdrawn from storage in the fat deposits of the body and used to supply energy. The average adult male has about 9 kilograms and the average adult woman about 11 kilograms, of stored fat (about 15 per cent and 21 per cent, respectively, of the total weight). The calories from the stored fat will supply energy for five to seven weeks of life. Finally, when the carbohydrate and fat reserves are used up, the body begins to consume its own structural materials, the proteins, first of the less essential organs, then of the essential ones (the brain, heart and other internal organs), until death occurs.

II. THE FUELS

2. Carbohydrates. Sugars and starches are the principal sources of energy in the ordinary human diet, but they are not essential to the body in any way; it could obtain energy as well from a mixture of protein and fat. Carbohydrates are the cheapest foods commercially, and the fact that the average diet contains large amounts of them is due primarily to this economic factor. In addition to sugars and starches, such substances as the citric acid of citrus fruits and the malic acid of apples and tomatoes are carbohydrates and serve as sources of energy.

3. Fats. Fats and oils are the most concentrated foods, since they not only supply more than twice as many calories per gram as carbohydrates and proteins, but also contain less water than these substances. They are digested and absorbed more slowly than other foods, so that one does not become hungry after a meal rich in fats as soon as after one of proteins and carbohydrates. However, meals that contain too high a proportion of fat are to be avoided, because the body is unable to oxidize fats completely unless a sufficient amount of carbohydrate is oxidized simultaneously.

Fats are broken down into glycerol and fatty acids. The body is able to synthesize most, but not all, of the fatty acids, and the few which cannot be synthesized must be taken in with the diet; hence they are called "essential." The required amounts of them are small, and provided by almost any diet. The fact that they are essential was discovered only when animals were raised on highly purified diets from which fat had been removed chemically. Fats and oils are important also because they contain fat-soluble vitamins.

4. Proteins. Proteins are the most expensive of the three types of fuels, and the amount of protein in the diet largely depends on the person's income. Because the body is constantly tearing down and replacing the protein in protoplasm, there must be a constant supply of protein in the food, even for adults whose growth has ceased and in whom there is no increase in the total amount of protoplasm. In growing children, pregnant women and people recovering from wasting diseases—in all people, that is, whose cells are manufacturing more protoplasm than is being destroyed each day—the protein intake must exceed the output. It is difficult to say just how much is necessary in the diet

to maintain health, since that depends on the kind eaten and the amount of other substances in the diet. You will remember that proteins are made up of smaller units known as amino acids, of which there are twenty-five different kinds. Proteins differ widely in the number and kind of amino acids they contain. When the body cells are synthesizing a particular type of protein, all the specific amino acids which make it up must be available. If they are not, or are present in inadequate amounts, the protein cannot be made. Animal cells can manufacture certain amino acids, but not all of them, and the ones they cannot synthesize, called "essential amino acids," must be supplied in the diet. There are ten of these essential amino acids, and proteins which contain all of them in adequate amounts are called "adequate proteins." Milk, meat and eggs contain biologically adequate proteins, but the protein in corn (zein) lacks two essential amino acids, so that an animal raised on a diet of which corn is the sole source of protein, loses weight and dies. If the two amino acids, tryptophane and lysine, are fed in addition to zein, normal growth takes place. Gelatin lacks three of the essential amino acids. By eating a mixture of different proteins, one avoids any danger of suffering from a deficiency of any of the essential amino acids. But since the diet must contain an adequate quantity of all the essential ones, the total amount of protein necessary to maintain health is that which provides a sufficiency of even the least plentiful. Experiments have shown that it is possible for an adult to maintain health on as little as 25 gm. of protein per day, but larger amounts, from 70 to 100 gm., are desirable. If an excess of protein is ingested it is converted into fat or carbohydrate to be stored, or used for energy.

The element nitrogen is found in proteins, but not in carbohydrates or fats, and by measuring the amount of it in the urine and feces and in the food ingested, it is possible to determine whether or not the body is maintaining nitrogen and therefore protein equilibrium.

Soon after protein is eaten, the metabolic rate increases temporarily to as much as 30 per cent above the basal level, which is believed to represent the energy necessary to change some of the amino acids into carbohydrate or fat. This phenomenon is called the **specific dynamic action** of proteins. It depends upon some action of the liver on the amino acids, for if protein is fed to an experimental animal whose liver has been removed, the metabolic rate does not increase.

III. THE METABOLISM OF CARBOHYDRATES, FATS AND PROTEINS

In the previous chapter we traced the history of foods from the mouth to their absorption through the wall of the small intestine—proteins and carbohydrates being absorbed into the capillaries of the villi, and fats by way of the lymph vessels of the villi. After absorbtion the amino acids and simple sugars are carried to the liver by way of the hepatic portal vein. Perhaps, originally, the liver was important in digestion only, but during the evolutionary process it assumed many other functions and is now a chemical jack-of-all-trades. It protects the body by detoxifying certain harmful substances; it is active in the storage and interconversion of carbohydrates, fats and proteins; it is important in the metabolism of hemoglobin; it stores certain vitamins; it manufac-

tures substances necessary for the coagulation of the blood; and it converts some of the harmful waste products produced by the metabolism of other body cells to less harmful, more soluble ones which can be excreted by the kidneys.

5. Carbohydrate Metabolism. Three kinds of simple sugars—glucose, fructose, and galactose—are derived from the breakdown of different kinds of double sugars and are absorbed from the digestive tract. From there they pass to the liver, which converts the other simple sugars to glucose and stores them all as **glycogen.** Glycogen is nothing more than a collection of glucose molecules bound together chemically for storage.

The role of the liver in storing carbohydrates was discovered by the French physiologist, Claude Bernard. He analyzed the glucose content of blood entering and leaving the liver just after a meal and found a much higher concentration of sugar in the blood entering the liver than in that leaving it. Analysis of the liver showed that new glycogen appeared simultaneously. Later the liver reconverts the glycogen to glucose with a resulting higher concentration of glucose in the blood leaving the liver than in that entering it. In this way Bernard discovered that the liver keeps the glucose concentration of the blood more or less constant, throughout the day.

The liver can store enough glycogen to supply glucose for about twelve to twenty-four hours; after that it must maintain the normal glucose level of the blood by converting other substances, principally amino acids, into glucose. If the supply of protein is sufficient, up to 60 per cent of the amino acids ingested can be converted by the liver into glucose.

Since glucose is the primary source of energy for all cells, its concentration in the blood must be maintained above a certain minimum level, about 60 mg. per 100 cc. of blood. The brain is the first organ to suffer when the concentration falls below this, because in contrast to most other cells of the body, the brain cells are unable to store any appreciable quantity of glucose and they cannot use fats or amino acids as sources of energy. When the glucose level is low, the diffusion of this substance from the blood stream into the cells where it is oxidized is not fast enough to supply the brain with adequate fuel. This results in symptoms similar to those accompanying a lack of oxygen—mental confusion, convulsions, unconsciousness and death. Whenever the brain cells (or any other cells) are deprived of either glucose or oxygen, they cannot carry on the metabolic processes which yield energy for their normal functioning. Other tissues normally get glucose for energy from the blood, but they can use other substances when necessary.

Muscle cells also can change glucose into glycogen for storage, but the muscle glycogen serves mainly as a local fuel deposit, available for muscular work, and is not important in regulating the blood glucose level.

Besides being stored as glycogen or oxidized for energy, glucose may be transformed into fat for storage. Whenever the supply of glucose exceeds the immediate needs, the liver converts it into fat, to be used for energy at some later time. It has been known for many years that eating large amounts of starches or sugars is fattening; thus starch in the form of corn or wheat eaten by cattle and pigs is converted into

the fat of butter and bacon. But only recently, with the use of radioactive or stable isotopes, has it been possible to demonstrate that a particular carbon or hydrogen atom put into the body as carbohydrate can be recovered in the fat of adipose tissue and liver.

The functioning of the liver in carbohydrate metabolism is regulated by a complex interaction of four hormones—one from the pancreas, one from the adrenal medulla, one from the adrenal cortex, and one from the pituitary.

6. Fat Metabolism. Each species of animal or plant deposits fat with particular kinds of fatty acids; hence when we eat beef fat or olive oil, it must be changed into the type of fat characteristic of human beings. This is done by the liver, which also converts the absorbed fat into a form which can be stored in adipose tissue. The fat in such tissue, besides being available as a source of energy when needed, serves as a supporting cushion for certain internal organs and as an insulating layer under the skin, preventing too rapid heat loss. The liver also partially breaks down fats so that they can be oxidized by other tissues. There is evidence that unless glucose is being metabolized at the same time, the oxidation of fats does not occur properly.

Diabetics, in whom the metabolism of carbohydrates is interfered with, have abnormal fat metabolism also, and certain injurious intermediate products (called acetone bodies) resulting from the breakdown of fats tend to accumulate in their blood. In addition, large amounts of fat collect in the liver, a symptom which occurs in certain other abnormalities of liver function.

Fats, as well as proteins, make up the structure of protoplasm, especially the nuclear and plasma membranes, to which they give the property of semipermeability.

Fat metabolism is controlled partly by hormones from the pituitary and adrenals, and partly by sex hormones, but the details of this regulation are not clear. Any severe disturbance of liver function results in the almost complete absence of fat from the usual adipose tissues, indicating that fat must be acted upon in some way by the liver before the body can use it for storage or as a source of energy.

7. Protein Metabolism. Most of the amino acids entering the liver from the hepatic portal vein are removed from the blood and stored temporarily. Later, some of them are returned to the blood and carried to other cells to be incorporated into new protoplasm. Recent experiments, using amino acids labeled with the isotope N^{15}, or "heavy" nitrogen, have shown that the body proteins are constantly and rapidly being torn down and rebuilt.

If there are more amino acids in the diet than are necessary to maintain the protoplasm, liver cell enzymes remove the amino group from amino acids, a process called **deamination.** Other enzymes, by combining the split-off amino groups with carbon dioxide, convert them into a waste product, urea, which is carried by the blood stream to the kidneys and eliminated in the urine. The parts of the amino acids remaining after deamination are simple organic acids, converted by the liver either into glucose and glycogen to be used for energy, or into stored fat. There is little or no storage of proteins as such in the body;

the proteins the body draws upon when carbohydrates and fats are exhausted are not stored proteins, but are the actual substance of the protoplasm of the cells.

The hormonal control of protein metabolism is even more obscure than that of lipids. Since growth is essentially the deposition of new protein in protoplasm, the growth hormone of the pituitary plays some part in it, but its nature is unknown. One of the hormones from the adrenal cortex is also involved in the control of protein metabolism.

IV. OTHER COMPONENTS OF THE DIET

8. Minerals. Some fifteen elements are known to be essential as mineral salts in the diet, of which a few are needed only in traces.* The constant loss of mineral salts from the body (about 30 gm. per day) in the urine, sweat and feces must be balanced by the intake of equal amounts in the food. A diet that contains no minerals is more rapidly fatal than no food at all, because the excretion of wastes from the metabolism of carbohydrates, fats and proteins requires the simultaneous excretion of a certain amount of salt (to keep the *p*H of the blood constant). Thus, a salt-free diet actually exhausts the body reserve of salts. Deficiencies of minerals are rather rare, since meat, cheese, eggs, milk and vegetables are rich sources of them. But deficiencies of iron, calcium and iodine do occur.

Since blood and other body fluids are about 0.9 per cent salt, and most of this is sodium chloride (common table salt), sodium and chlorine are important in maintaining osmotic balance in the body. These elements are important components of the secretions of the digestive tract—the hydrochloric acid of the stomach, and the pancreatic and intestinal juices. The salts in these secretions are reabsorbed and used over again, so that the loss of salts via the digestive tract is negligible. The daily requirement for sodium chloride varies widely and depends on the amount lost in perspiration. Men doing heavy work in hot places— for example, "sand hogs" digging tunnels—must drink salt water instead of plain water, or the amount of salt in the blood will decrease, resulting in muscular cramps and heat exhaustion.

Potassium and magnesium are necessary for muscle contraction, as well as for the functioning of many enzymes.

Calcium and phosphorus are the chief constituents of bones and teeth, and a deficiency in childhood of either one (or of vitamin D; see p. 224) produces rickets. Phosphorus is extremely important in carbohydrate and protein metabolism also; both types of substances must be changed into intermediate compounds containing phosphorus before they can be utilized as sources of energy.

Iodine is a constituent of the hormone of the thyroid gland, and if the diet is deficient in this substance, the gland is unable to make its hormone and the disease known as goiter (p. 311) results. Iodine is abundant in sea water and sea foods, but is rare elsewhere, and formerly it

* The daily requirement of some of these are as follows: sodium chloride, 2–10 gm.; potassium, 1–2 gm.; magnesium, 0.3 gm.; phosphorus, 1.5 gm.; calcium, 0.8 gm. (more during growth or pregnancy); iron, 0.012 gm.; copper, 0.001 gm.; manganese, 0.0003 gm.; iodine, 0.00003 gm.

was common for people living in inland regions to suffer from goiter. Now, most table salt is fortified with small amounts of potassium iodide to prevent this.

Iron is found in the body in hemoglobin and in certain respiratory enzymes (cytochromes). This iron is used over and over, and as long as there is no loss of blood the amount of iron needed daily in the diet is negligible. Because women lose a considerable amount of blood each month by menstruation, they are more likely to become anemic, due to an iron deficiency, than are men.

Small amounts of copper are necessary in the diet to bring about the proper utilization of iron, and for normal growth. Traces of manganese, zinc and cobalt are also required for normal growth, but their functions are not all known. Zinc is a constituent of the enzyme carbonic anhydrase.

9. Water. Water makes up about two thirds of the human body and is an essential component of every cell. It is the fluid part of blood and lymph, and is the medium in which the other chemicals are dissolved and in which all chemical reactions occur. It is indispensable for digestion, since the splitting of carbohydrates, proteins and fats requires a molecule of water for each pair of sugar molecules or amino acid molecules separated. Water removes metabolic wastes, distributes and regulates body heat, and, as perspiration, cools the body surface. The amount of water lost daily averages about 2 liters, although it varies with individual activities and the climate. The loss must be replaced promptly; men can live weeks without food, but only a few days without water. All foods contain some water, and some, such as green vegetables and fruits, may contain as much as 95 per cent water.

10. Condiments and Roughage. Pepper and other spices, collectively known as condiments, have little or no food value themselves, but are important for making foods more palatable. By stimulating the appetite they help insure that a sufficient quantity of food is eaten.

We have already discussed the importance of "bulk" or undigested matter in stimulating the movements of the intestines and preventing constipation. The diet should contain some indigestible matter for this purpose, such as the cellulose material from vegetables and fruits.

11. Vitamins. One of the most notable biochemical achievements since the turn of the century has been the discovery of vitamins and the analysis of their properties. Vitamins are relatively simple organic compounds which, though present in such scanty amounts that they cannot be used as sources of energy, are absolutely essential to life. The various vitamins are quite different chemically, but are similar in that they cannot be manufactured by the animal body and therefore must be present in the diet in small amounts for metabolism to occur normally. When an adequate amount of any one of them is not present, a specific pathological condition or deficiency disease occurs, curable only by administration of the specific vitamin; for example, only vitamin C is effective in curing scurvy.

In 1912, investigators found that animals could not survive on a diet of purified carbohydrates, proteins and fats, but that accessory growth factors or vitamins were necessary. Since at first the chemical structure

of these substances was unknown, they were referred to as vitamins A, B and C, which prevented night blindness and rickets, beriberi, and scurvy, respectively. Today, the chemical structure of nearly all of them is known, and most of them have been made synthetically. The original vitamins A and B are complexes of several vitamins, A being subdivided into A, D and E, while vitamin B consists of almost a dozen different ones. The vitamins of known chemical structure are usually referred to by their chemical name; e. g., thiamine rather than vitamin B.

The distinction between vitamins and such things as essential amino or fatty acids is not clear cut; the latter are also simple organic substances, essential for life, which cannot be made by the animal body and must be taken in with the food. They are needed in much larger amounts, however; the term vitamin is reserved for the substances required by the body in very small quantities.

The average adult eating a normal varied diet has no need to take vitamin pills; he will obtain the necessary kinds and amounts of vitamins from his food. Infants and younger children, whose diets are more restricted, may need supplementary amounts of certain vitamins, especially A and D. The vitamin requirements of different animals are not the same; most animals do not require vitamin C, since it is made in their own bodies; only man, monkeys and guinea pigs need it in their diet. For insects, only the B complex vitamins are necessary.

Thus, what is a vitamin for one animal is not a vitamin for another, although it is probable that all animals and plants require all or nearly all the known vitamins. In the few cases where the exact function of a vitamin has been traced, it is known to act as a catalyst for some fundamental reaction common to all protoplasm. The clearest demonstration of this has been provided by the experiments of Beadle and Tatum and their collaborators on the baker's mold, *Neurospora*. The ordinary "wild" strain of this mold requires in its culture medium only a single vitamin, biotin, in addition to salts and a sugar of some sort. By exposing mold organisms to x-rays or ultraviolet light, thus causing a gene mutation which made the synthesis of a vitamin impossible, these investigators produced mutant strains which would grow only when one additional vitamin was added to the culture medium. Now there are strains which require each of the vitamins necessary for growth in animals. This is evidence that the mold cells (and probably other plant cells) need these substances for growth just as much as animal cells do, but that ordinarily they synthesize all the vitamins they need except biotin.

It is quite likely that the ancestors of animals also had the ability to synthesize all the substances we now call vitamins, but that over the intervening millions of years, mutations occurred which interfered with the synthesis of these substances, so that to survive, the organisms had to obtain the compounds in their diet. And since, in different evolutionary lines, a variety of mutations have occurred, the species living today have different vitamin requirements. If such mutations occurred in a green plant, the plant would die, having no way of obtaining the vitamin.

Vitamin A. Vitamin A occurs only in animal products such as butter,

eggs and fish liver oils, but plants contain a yellowish substance, called **carotene** or provitamin A, which is easily changed into vitamin A in animal cells. Vitamin A itself is fat-soluble and can be stored in the body. The daily requirement for adults is about 1.5 mg. (5000 International Units), for a child under three about 0.6 mg., and for older children an intermediate amount.

Fig. 104. *A*, Typical eye condition produced by lack of vitamin A. *B*, The eyes restored to normal by the feeding of 3 units (about 0.001 mg.) of vitamin A daily. (Courtesy of E. R. Squibb and Sons.)

This vitamin is necessary for the maintenance of the epithelial cells of the skin, eye, digestive and respiratory tracts. When there is a deficiency, these cells become flat, brittle and less resistant to infection than normal (vitamin A is sometimes called the anti-infection vitamin). In advanced cases of the deficiency the eye epithelium forms a dry and horny film over the cornea, resulting in a characteristic type of blindness

called **xerophthalmia** (Fig. 104). Vitamin A is necessary also for the maintenance of normal nerve tissue and for the growth of bone and the enamel of teeth. It is involved in the chemistry of vision, so that **night blindness,** inability to see in a dim light, may be due to vitamin A deficiency. The retina of the eye contains a substance called **visual purple,** made up of vitamin A and a protein; this is broken down when light strikes it, stimulating the receptor cells which send impulses to the brain, resulting in the sensation of sight. Ordinarily, this substance is quickly rebuilt, but when insufficient vitamin A is present, the reconstruction of visual purple is retarded and night blindness results. De-

Fig. 105. A child with rickets. A deficiency of vitamin D decreases the ability of the body to absorb and use calcium and phosphorus in bone formation, resulting in soft, malformed bones. (Cooper, Barber and Mitchell: Nutrition in Health and Disease for Nurses, J. B. Lippincott Co.)

ficiencies severe enough to produce xerophthalmia are rare in the United States, but night blindness is more common. During World War II, the pilots of night fighter planes were fed diets particularly rich in vitamin A to prevent this.

Vitamin D. Another fat-soluble vitamin, D, or *calciferol,* is unique in that it can be made in the body under the influence of sunlight (it is sometimes called the "sunshine" vitamin) from a substance called ergosterol normally present in the skin. Calciferol is also found in liver oils, butter, eggs and milk, and any excess manufactured in the skin during the summer months is stored in the liver. This substance is necessary for the normal absorption of calcium and phosphorus from the intestine; about 0.02 mg. per day is recommended for children and adults. When there is a deficiency of calciferol, calcium and phosphorus are not ab-

sorbed in normal amounts, so the formation of bones and teeth is retarded for lack of raw material. This results in the disease known as **rickets** (Fig. 105), characterized by soft, weak bones, enlarged ankles, knees and wrists, bowing of the legs, beaded ribs, and defective tooth development. There is danger in overdosing a person with vitamin D, however, because it may lead to calcification of the soft tissues and death.

Fig. 106. A person suffering from scurvy, the disease caused by a deficiency of vitamin C. Note the many hemorrhagic spots produced by the breaking of blood vessels under the skin. The fragility of the capillaries in vitamin C deficiency causes similar bleeding of the gums, tongue and cheek, as well as painful, stiff joints. Harris: Vitamins in Theory and Practice, Cambridge University Press.)

Vitamin C. The deficiency disease **scurvy**, resulting from a lack of vitamin C, is one of the principal noninfectious plagues of history, characterized by bleeding gums, bruised skin, painful swollen joints, and general weakness (Fig. 106). It occurs whenever people are deprived of fresh fruits, vegetables and meat for long periods of time, as they are on extended sailing voyages or during the long northern winters. Modern methods of preserving and shipping foods have practically eliminated this disease, but slight deficiencies, characterized by laziness, gloom and irritability, still occur.

The scurvy-preventing vitamin was isolated in 1933 and proved to be ascorbic acid (or hexuronic acid), a substance that had been known

for many years, but whose antiscorbutic properties had not been suspected. Ascorbic acid is rather unstable and is rapidly destroyed by cooking, so that the best sources of it are fresh fruits and juices, although modern canning processes preserve most of the ascorbic acid content of food. The exact role of ascorbic acid in metabolism is unknown, but it plays some part in the constantly occurring cellular oxidations, and it assists in the oxidation of one of the amino acids, tyrosine. It is also necessary for the maintenance of normal connective tissue. In its absence the capillaries become exceedingly fragile and easily ruptured, resulting in hemorrhages under the skin and in the joints. The development of bones and teeth also is abnormal. Normal human adults require between 75 and 100 mg. of ascorbic acid daily, an amount supplied by an eight-ounce glass of orange juice.

Vitamin E (Alpha Tocopherol). Recent experimental studies on rats, chicks and ducks have proved the existence of vitamin E, or alpha tocopherol, which is necessary to prevent sterility. If it is absent from the diet, male animals become sterile, owing to degenerative changes in the testes, and females are unable to complete pregnancy successfully, since the embryos die and are resorbed. Eggs from vitamin E-deficient hens fail to hatch. So far it has not been shown that a deficiency of vitamin E is responsible for human sterility, but this is possible. No figure can be given for the daily human requirement of the substance, but it is so widespread in both vegetable and animal oils that a deficiency in any normal diet is almost impossible.

Experiments have shown also that a deficiency of vitamin E produces progressive deterioration of the muscles and paralysis, presumably by degeneration of the nerves (just as the destruction of nerves in infantile paralysis leads to the wasting of muscles and paralysis). Certain types of paralysis in human beings have been treated with vitamin E preparations, with beneficial results, and it has been claimed recently that vitamin E is effective in treating certain types of heart disease.

Vitamin K. Normal coagulation of blood, depending upon the manufacture of prothrombin by the liver, is connected with the specific action of a number of different chemicals referred to as vitamin K. These chemicals with the same effect occur in a variety of foods and are manufactured by the bacteria in the human intestine, so that vitamin K deficiency in man usually results from some abnormality in its absorption rather than the lack of it in the diet. Since it can be absorbed only in the presence of bile salts (vitamins A, D and E also require bile salts to be absorbed), an obstruction of the bile duct results in vitamin K deficiency, no matter how much is present in the diet or made by the intestinal bacteria. Patients with vitamin K deficiencies are poor surgical risks because of the likelihood of hemorrhages after the operation; the administration of vitamin K (and bile salts, if necessary) before operation removes this danger and has saved many lives. Newborn infants, before they acquire their quota of intestinal bacteria, are likely to be deficient in vitamin K, and administration of this substance to the mother in the last few days of pregnancy helps prevent the hemorrhages that often occur in infants after delivery. No estimate can be given of the daily requirement of this vitamin, but in vitamin K deficiencies, 1

to 5 mg., administered daily, bring the clotting time of the blood back to normal.

The Vitamin B Complex. The original vitamin B was characterized as the anti-beriberi factor, but from the same extracts of liver, yeast or rice hulls which yield an anti-beriberi substance, nine other materials

Fig. 107. *A*, Polyneuritis (beriberi) in a rat raised on a diet deficient in thiamine. Note that the back is arched and the hind legs are stretched and far apart. Such animals have a peculiar halting gait and are particularly awkward in turning, readily losing their balance. When rotated, they have great difficulty in regaining equilibrium, probably because of degeneration of the nerves to the semicircular canals. *B*, The same rat eight hours after receiving an adequate dose of thiamine: the back and hind legs are normal, and the animal readily regains equilibrium when spun. (Courtesy of the Upjohn Company.)

with specific biological effects have been separated. Some of these substances were once given separate alphabetical designations: riboflavin was called vitamin G, and biotin was called vitamin H, but they are now all grouped together as members of the B complex, not because they are similar chemically or in their effects, but because they tend to occur together. Individual members of the B complex are referred to by their chemical names.

Thiamine (Vitamin B_1). This substanee, the first to be separated from the rest of the eomplex, prevents beriberi. It is a white, erystalline material with a yeastlike odor, found in small quantities in a wide variety of foods. Yeast, liver, nuts, pork and whole grain eereals are the best

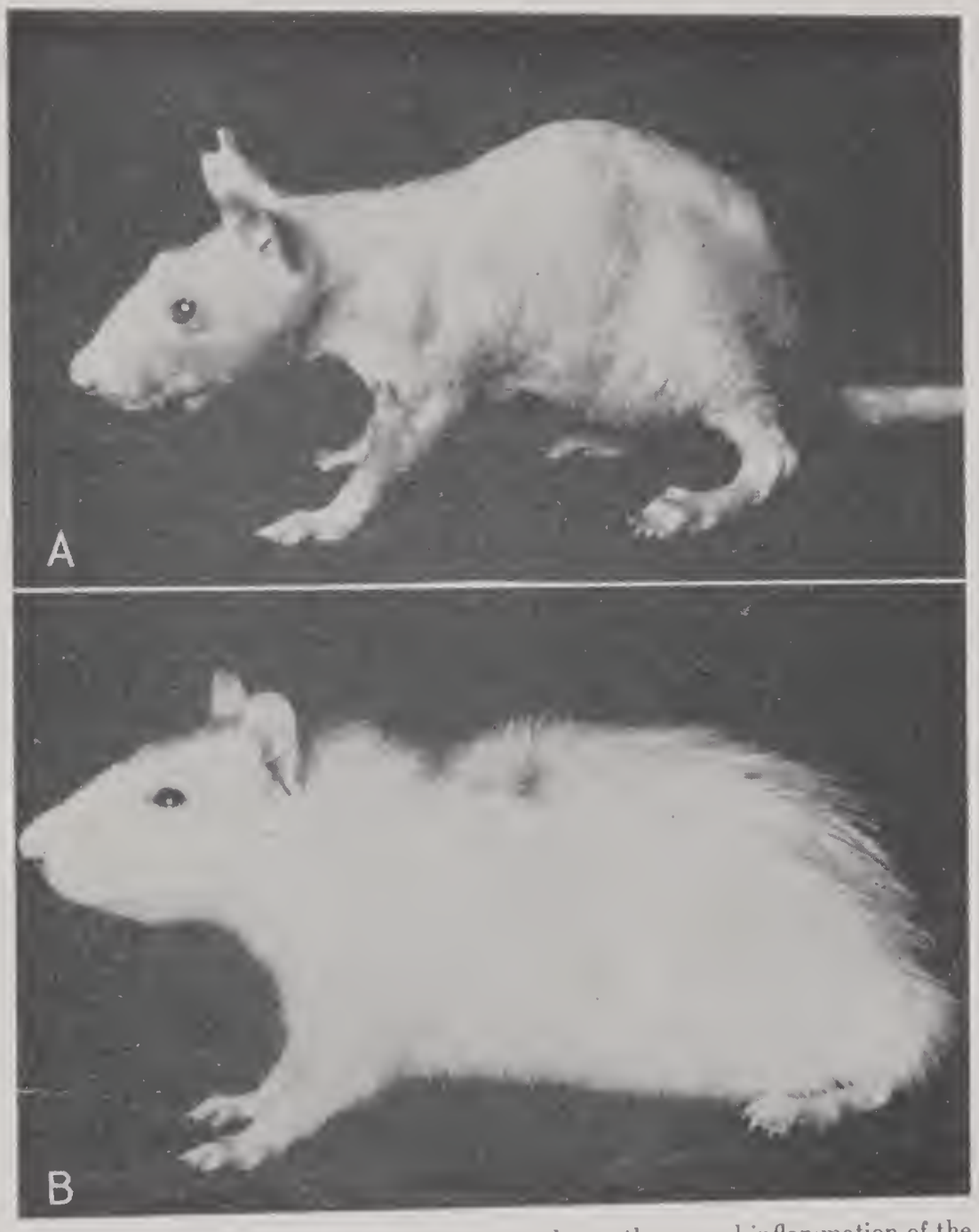


Fig. 108. *A,* Riboflavin-deficient rat, with stunted growth, general inflammation of the skin (note the open sore on the left front leg), scanty hair, and inflammation of the eyes. *B,* The same rat after two months of treatment with riboflavin: no signs of the deficiency are visible; growth has been resumed, and the lesions of the skin and eyes are cured. (Courtesy of the Upjohn Company.)

sourees of all the vitamin B eomplex. Sinee the average Ameriean diet is somewhat defieient in thiamine, flour, bread and breakfast eereals are now enriehed with it. The daily requirement varies with the body weight, the number of ealories eaten, and the proportion of earbohydrate in the diet (the more earbohydrate, the more thiamine needed), but the amount needed daily by the average person is from 2 to 3 mg. It is now prepared synthetieally in large quantities, and the priee has

dropped from about $1000 a gram (1935) to $0.16 a gram (1950). Thiamine and the other B complex vitamins are not stored in the body to any great extent, and evidence of a deficiency appears within a few weeks. Most diets contain enough thiamine to prevent the appearance of beriberi, but may not contain enough for maximum health.

The function of thiamine in the body is to form the active part or "coenzyme" of a particular enzyme involved in the metabolism of carbohydrates. When a thiamine deficiency interferes with carbohydrate metabolism, a number of characteristic symptoms appear: in mild deficiencies there is fatigue, loss of appetite, weakness and muscular cramps; in more marked deficiencies these symptoms are accentuated, and there is also a painful degeneration of the nerves and a secondary wasting of the muscles resulting in paralysis. This condition is known as **beriberi** (Fig. 107). The symptoms disappear rapidly when thiamine is given. Any diet deficient in thiamine is likely to be deficient in the other B complex vitamins as well, so that cases of thiamine deficiency alone are rare.

Fig. 109. Pellagra in a child, showing typical inflammation of the skin of the exposed areas, the hands and face. (Courtesy of Dr. John A. McIntosh.)

Riboflavin (Vitamin B_2 or G). Riboflavin is a yellow pigment found in both plant and animal tissues; it occurs most abundantly in foods rich in thiamine: yeast, liver, wheat germ, meat, eggs and cheese. It resembles thiamine in being a coenzyme concerned in carbohydrate metabolism and in cell oxidative processes. One to 2 mg. of riboflavin per day are required to maintain health in man. A deficiency of riboflavin is marked by the appearance of cracks in the corners of the mouth, a characteristic purplish-red color of the tongue, and stunted growth. In experimental riboflavin deficiencies in rats there is failure of growth, loss of hair, cataract, inflammation of the eyes, and death (Fig. 108).

Niacin or Nicotinic Acid. Niacin is a substance that forms two different coenzymes which are the active parts of many different enzymes in cellular metabolism. Niacin was known as an organic compound for over fifty years before its function as a vitamin was recognized. It is found in yeast, fresh vegetables, meat and beer. Corn meal has an unusually low niacin content, and wherever this food forms a large part of the diet, the deficiency disease **pellagra** is fairly prevalent. Pellagra (Fig. 109) is characterized by dermatitis (reddened inflammation of the skin, especially in those parts of the body exposed to light), diarrhea and dementia. The normal functions of niacin are, then, the main-

tenance of the epithelia of the skin and digestive tract and of normal nerve functioning—processes carried on by its action as the coenzyme of one or another of many different enzymes. The recommended daily allowance of niacin is about 20 to 25 mg., but a considerable part of the human requirement comes from a bacterial synthesis of it in the intestine. When a person is treated with sulfa drugs for some infection, the intestinal bacteria are killed and deficiencies of a number of vitamins, including niacin, may occur.

The original name for this substance was nicotinic acid, since it is related chemically to nicotine, but because the two are confused, the name niacin is now being adopted.

Pyridoxine (Vitamin B_6). It has been known for some time that pyridoxine is necessary in the diet of rats, and it is now believed that human beings also require it. The vitamin occurs in a wide variety of foods—meat, eggs, nuts, whole grain cereals, and beans—so that a clear-cut deficiency of pyridoxine in man has not been found. A derivative of it, pyridoxal phosphate, is the coenzyme for two important enzyme systems, one of which is involved in the synthesis of fat from protein. Experimental animals fed a diet deficient in pyridoxine fail to grow, become anemic and have atrophied lymph tissue, resulting in a lack of white blood cells and antibodies, with a consequent lowered resistance to infection. The administration of pyridoxine has been tried in a number of human disorders, but without consistent results. The daily requirement is about 1 to 2 mg., but it varies with the amount of protein in the diet, since the more protein eaten, the more pyridoxine is needed to stimulate growth.

Pantothenic Acid. This vitamin is necessary for the maintenance of normal nerves and skin, and experimental deficiencies of it cause the failure of growth. There is no report of a deficiency of pantothenic acid in man, because it is widely distributed in foods and almost any diet provides the 20 mg. required daily by human beings. Especially rich sources of it are eggs, meat, sweet potatoes and peanuts. It forms part of another coenzyme, called "coenzyme A," important in carbohydrate metabolism.

Biotin (Vitamin H). This was first discovered as a factor indispensable for the growth of yeast. It has since been shown to be necessary in the diet of mammals, though only in extremely small amounts. Some rich sources of it are molasses, egg yolk and liver. Egg white contains a protein called **avidin,** which combines with biotin in the intestine and prevents its absorption. Avidin is destroyed by heat, however, so that cooked egg white does not interfere with the absorption of biotin, and much more than the amount in an eggnog or two is needed to cause biotin deficiency in experimental animals. One of the few cases of human biotin deficiency occurred in a man who lived almost entirely on raw eggs and wine and suffered an inflammation of the skin; it cleared up when biotin was administered. Biotin forms a coenzyme which is necessary for the utilization of carbon dioxide in certain body processes.

Folic Acid, Vitamin B_{12}, Choline, Inositol and Para-Aminobenzoic Acid. These substances are also members of the B complex. Folic acid

and vitamin B_{12} are necessary to prevent anemia and are used in conjunction with liver extract in treating pernicious anemia (p. 135).

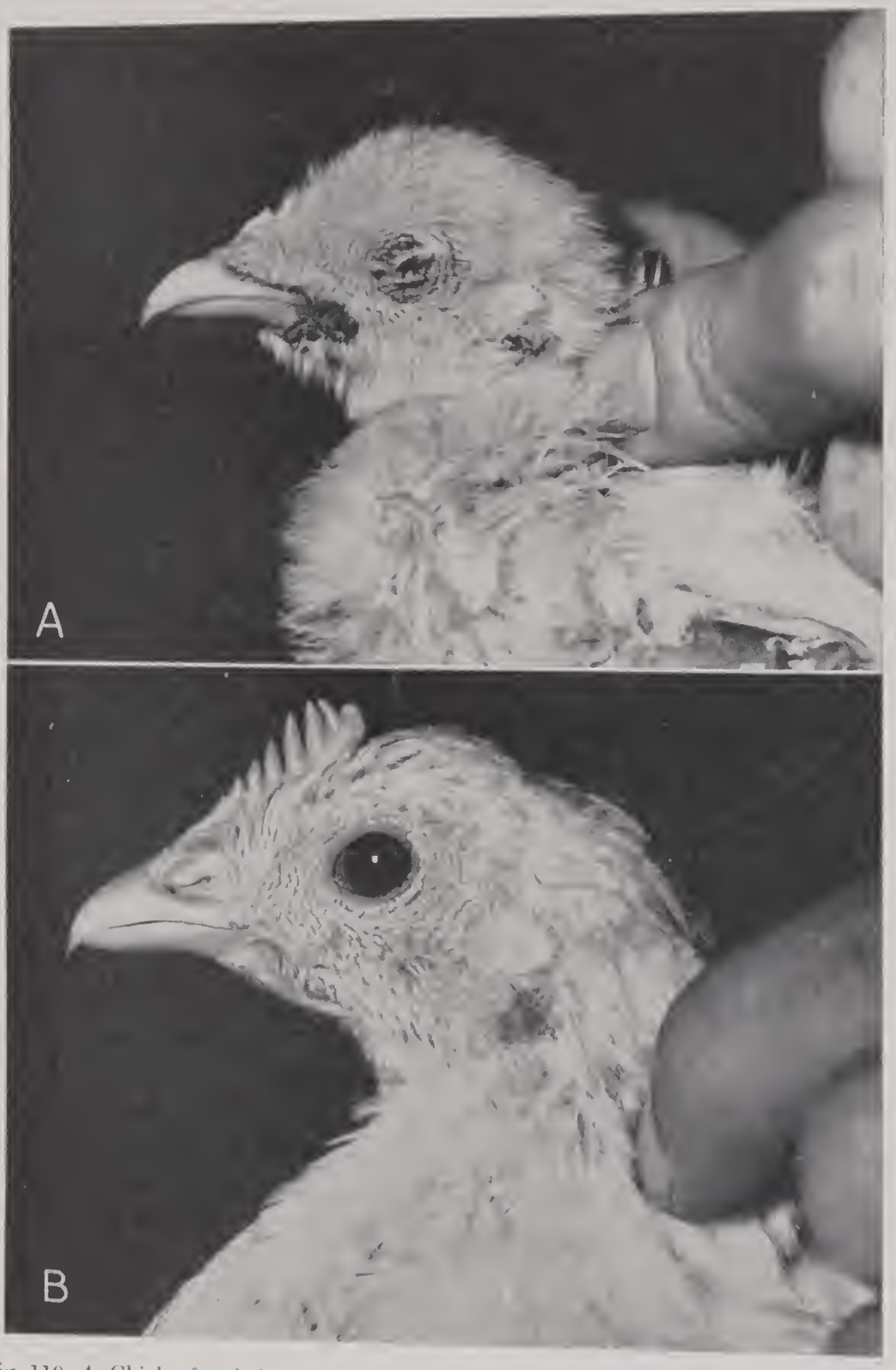


Fig. 110. *A*, Chick after being fed a diet deficient in pantothenic acid (one of the B complex vitamins). The eyelids, corners of the mouth, and adjacent skin are inflamed. The growth of feathers is retarded, and the feathers are rough. *B*, The same chick after three weeks on a diet with pantothenic acid: the lesions are completely cured. (Courtesy of the Upjohn Company.)

Choline is a growth factor the absence of which causes hemorrhages in the kidneys and a bone deformity in chicks called perosis. It is im-

portant in the metabolism of fats and proteins, not as a coenzyme as many other B vitamins are, but as a source of methyl groups to be used in building up certain essential substances. An adult requires about 2000 mg. of choline daily.

Fig. 111. *A*, Rat after being fed a diet deficient in biotin, to which raw egg white was added. Growth has been retarded, and there is generalized inflammation of the skin. *B*, The same rat after three months on a diet containing adequate amounts of biotin: growth is normal and the skin lesions are completely healed. (Courtesy of the Upjohn Company.)

Inositol and para-aminobenzoic acid have been reported as important in preventing the loss of hair and the graying of hair, respectively. Both are necessary for normal growth of rats and presumably of other animals, including man. These five B vitamins are also synthesized by the intestinal bacteria.

V. DIET

Unfortunately, many people believe (or rationalize themselves into believing) that good health is associated with the eating of tremendous quantities of food. The error seems to be especially prevalent among parents, who urge second and third "helpings" on already plump children, and in some cases, even go so far as to run races with them to see who can eat the most. Actually, almost nothing could be more detrimental to a child's future health and happiness than to overeat and so gain weight in excess of what is proper for his age. For in later years this fat—too often not lost—puts a strain upon the whole body, particularly the heart and kidneys, and may lead to or aggravate innumerable diseases.

The problem of the relation between diet and health has been tackled with extremely interesting and significant results by Dr. Clive M. McCay of Cornell University. Working primarily with rats, hamsters and dogs, Dr. McCay has found that a low-calorie diet, particularly during the early years of life, has the effect of doubling the animals' lives. And not only are the experimental animals longer-lived—they are spryer, sleeker, more fertile and healthier right up to the time of death, which occurs suddenly with no lingering and painful effects. The statistics on these experiments prove what animal breeders and trainers have long known—that an animal looks and behaves better when it is slightly underfed.

There is every indication that what is true for rats and dogs is true for human beings. Many physiologists, by performing experiments on themselves, have found that a restricted diet produces beneficial psychological effects: they felt more alert, happier, and able to stick to tedious, problem-solving tasks much longer. It is to be hoped that all these discoveries will receive wide publicity and attention, for the truth seems to be that the American public is spending enormous sums on too much of the wrong kind of food, thereby ruining its health, efficiency and appearance.

An adequate diet must supply water, salts and vitamins; sufficient calories to balance the daily expenditure of energy (unless one wishes to lose weight); and enough fats and proteins for tissue repair. Except where there is extreme poverty, ignorance, idiosynerasy of taste or some accidental factor which prevents the eating of a normal diet, there is little danger of anyone's failing to obtain the specific, essential substances. A daily diet including two or three glasses of milk, an egg, one or two servings of lean meat, plenty of green and yellow vegetables, fresh fruit, whole grain cereals and bread, with moderate servings of butter or margarine, and a glass of citrus fruit, will provide adequate amounts of all the necessary foods. The more fresh—and especially raw—vegetables, and the fewer fried foods, pastries, rich sauces, whipped cream and candy,* the better. Table 7 gives the nutritional content of many common foods and how many calories they contain.

* The latest research in the field of dental health indicates that sweets of all kinds are the greatest factor in producing caries. In children particularly, there is an unmistakable correlation between high sugar consumption and a large number of cavities.

Table 7. Analyses of Common Foods

(From Bowes and Church)

Food	Wt. (gm.)	Approximate Measure	Protein (gm.)	Fat (gm.)	Carbohydrates (gm.)	Calories	Calcium (mg.)	Phosphorus (mg.)	Iron (mg.)	Vitamins					
										A (I. U.)	Thiamine (mcg.)	Riboflavin (mcg.)	Niacin (mg.)	Ascorbic Acid (mg.)	D (I. U.)
BREADS															
Bread, white, enriched	25	1 slice, average	2 1	0 5	13 1	65	14	25	0 5		60	37	0 55		
Bread, whole wheat, 60%	28	1 slice, average	2 5	0 8	13 8	72	14	42	0 6		84	49	0 90		
Doughnut, yeast	30	1 small, 3″ diam.	2 0	6 5	14 0	123	13	24	0 4	51	67	56	0 50		1
Griddle cakes, white	50	1 medium, 4″ diam.	2 4	2 4	11 1	76	32	38	0 4	110	62	78	0 42		2
Roll, white, hard	35	1 av., no milk or butter	2 9	2 1	18 9	106	20	35	0 6		84	53	0 77		
CEREALS															
Corn flakes, Kellogg's	28 35	1 oz., 1 1/3 cups	2 2	0 1	24 5	107	1	11	0 5		120		0 60		
Oats, Quaker	30	2/3 cup, cooked	4 9	2 0	19 4	105	15	131	1 2		204	39	0 33		
Rice, white	30	3/4 cup, cooked	2 3	0 1	23 8	105	3	28	0 2		15	9	0 42		
Spaghetti, tomato sauce	220	1 serving	6 4	11 3	35 8	271	23	80	1 0	1,336	125	76	1 57	19	
Wheaties	28 35	1 oz., 1 cup	3 1	0 5	22 5	107	9	100	1 3		150	37	1 50		
CRACKERS AND SIMILAR PRODUCTS															
Crackers, saltines	4	1 cracker, 2″ square	0 4	0 5	2 8	17	1	4	0 06		2				
Pretzel	20	1 medium	1 8	0 6	14 9	72	7	26	0 3						
Ry-Krisp	6 5	1 piece	0 8	0 08	4 9	24	4	25	0 3		21	15	0 15		
DAIRY PRODUCTS															
Butter	10	1 pat, average	0 06	8 1	0 04	73	2	2	0 02	330		1	0 01		4
Cheese, American	28 35	1 oz., average serving	6 8	9 2	0 5	112	247	173	0 2	493	11	142	0 06		
Cheese, cottage	100	1/2 cup	19 2	0 8	4 3	101	82	263	0 5	30	20	290	0 10		
Ice cream, plain	100	1/6 quart, av. serving	4 0	12 3	20 8	210	132	104	0 1	540	40	190	0 10	Trace	
Milk, whole	180	6 oz., 1 medium glass	6 1	7 0	8 8	123	212	167	0 13	288	72	306	0 18	2	4
Egg, boiled	50	1 medium	6 4	5 8	0 4	79	27	105	1.4	570	52	161	0 05		45

FISH															
Halibut steak	100	1 serving	18 6	5 2		121	11	209	0 9	10	90	65	3 00		
Oysters, with liquor	100	4 to 6 medium	6 0	1 2	3 7	50	68	172	7 1		180	230	1 20	2	5
Salmon, canned, red	100	1 cup	20 5	6 2		138	194	289	1 3	325	30	225	6 50		800
FRUITS AND FRUIT JUICES															
Apple, fresh	150	1 large	0 5	0 6	22 5	97	9	15	0 5	135	60	30	0 30	8	
Banana, fresh	100	1 medium	1 2	0 2	23 0	99	8	28	0 6	430	90	60	0 60	10	
Orange juice, fresh	100	$^1_2$ cup			10 1	40	33	23	0 4	190	80	30	0 20	49	
Prunes, stewed	100	4 to 5 medium	1 1	0 3	40 5	169	27	43	1 9	945	50	80	0 85	1	
Tomato juice	100	$^1_2$ cup	1 0	0 2	4 3	23	7	15	0 4	1,050	50	30	0 70	16	
Watermelon	600	1 slice, 6″ x 1 $^1_2$″	3 0	1 2	41 4	188	42	72	1 2	3,540	300	300	1 20	36	
MEATS															
Bacon, cooked	30	3 strips, 5″ long, crisp	4 2	8 1	0 5	93	6	48	0 3		180	30	0 87		
Beef steak	115	1 pc., 4″ x 2″ x 1″	20 3	25 0		306	12	218	3 0		84	125	4 42		
Lamb chop	105	1 chop, 1″ thick	17 9	21 0		261	12	192	2 6		180	224	4 96		
Liver, beef	41	1 slice	9 9	3 3	3 0	82	6	187	6 1	9,600	115	1,190	6 85	?	23
Pork chop, fried	70	1 chop, medium	16 4	18 3		230	10	180	2 5		876	170	3 76		
Veal cutlet, breaded	122	1 chop	24 8	18 0	5 8	284	23	272	4 1	114	168	350	7 15		9
POULTRY															
Chicken, fried	95	$^1_2$ medium	20 6	10 4		176	12	218	1 9	138	93	153	7 3		
Turkey	30	1 piece, lean	10 7	1 5		56	6	112	1 6		49	65	2 12		
NUTS															
Almonds, salted	15	10 to 12 nuts	2 7	8 0	2 8	94	38	71	0 7		38	101	0 69	Trace	
Peanut butter	15	1 tablespoon	3 9	7 2	3 2	93	11	59	0 3		30	24	2 43		
Walnuts, English	15	8 to 15 halves	2 3	9 7	2 3	106	12	57	0 3	9	77	20	0 18	Trace	
SWEETS															
Chocolate creams	13	1 average piece	0 5	1 8	9 4	56	?	10	0 06			7			
Hershey's milk chocolate	43	1 bar, 5 cents	3 2	14 5	23 8	238	86	89	1 1	64	44	219	0 14		43
Assorted jams, commercial	20	1 tablespoon	0 1	0 06	14 2	58	4	3	0 06	2	2	4	0 03	Trace	

Table 7. Analyses of Common Foods—Continued

(From Bowes and Church)

Food	Wt. (gm.)	Approximate Measure	Protein (gm.)	Fat (gm.)	Carbohydrates (gm.)	Calories	Calcium (mg.)	Phosphorus (mg.)	Iron (mg.)	Vitamins					
										A (I. U.)	Thiamine (mcg.)	Riboflavin (mcg.)	Niacin (mg.)	Ascorbic Acid (mg.)	D (I. U.)
VEGETABLES															
Beans, string, fresh	100	1/2 cup, cooked	2 4	0 2	7 7	42	65	44	1 1	630	80	100	0 60	19	
Beets, fresh, raw	100	1/2 to 5/8 cup, diced	1 6	0 1	9 6	46	27	43	1 0	20	30	50	0 40	10	
Carrots, raw	100	1 large	1 2	0 3	9 3	45	39	37	0 8	12,000	70	60	0 50	6	
Corn, sweet, canned	100	1/2 cup	2 0	0 5	16 1	77	4	51	0 5	200	20	50	0 80	5	
Potatoes, white, baked	139	1 medium large	3 0	0 2	28 7	129	17	84	1 1	30	153	60	1 76	22	
Spinach, fresh	100	2/3 cup, cooked	2 3	0 3	3 2	25		55	3 0	9,420	120	240	0 70	59	
Tomatoes, fresh	100	1 medium, ripe	1 0	0 3	4 0	23	11	27	0 6	1,100	60	40	0 60	23	
BEVERAGES															
Chocolate milk shake	342	1 regular	11 1	17 7	57 7	435	362	323	0 4	708	120	534	0 37	2	9
Coca-Cola	170	1 bottle			20 4	82									
Coffee, roasted	100	3 1/2 oz.									900	70	8 69		
Beer, lager, American	240	1 large glass	1 2		8 9	103					10	72	1 92		
DESSERTS															
Cake, chocolate, 2 layers	100	1 pc., vanilla icing	4 3	8 3	68 7	368	43	80	0 6	229	25	110	0 23		8
Pudding, bread, with raisins		1 serving	6 1	7 0	29 3	205	99	119	1 1	349	116	193	0 98		16
Pie, apple		1/6 medium pie	2 6	13 3	34 0	266	11	36	0 6	116	53	30	0 42	1	
MISCELLANEOUS															
Salad, gelatine with fruit	155	1 serving with lettuce	1 9	9 0	20 8	172	16	18	0 3	331	23	32	0 18	2	3
Sandwich, bacon, lettuce, tomato		1, white toast	7 0	20 2	24 1	306	38	97	1 5	776	232	115	1 78	12	7
Stew, oyster	325	1 1/2 cups	14 3	18 7	15 5	287	353	397	7 3	714	248	575	1 30		12
Soup, vegetable	140	3/4 cup	4 6	4 2	11 6	103	31	45	0 6	1,612	54	35	0 57	7	

QUESTIONS

1. What are the three functions of food?
2. Specify the six main types of food. Which of these produce energy?
3. What is a Calorie?
4. Why is a square of butter more fattening than an equal amount of bread or meat?
5. What is the basal metabolic rate? What are two pathological conditions which increase it?
6. What are "adequate" proteins?
7. What is meant by the specific dynamic action of proteins?
8. What is glycogen? What is its function in the body?
9. What is the primary source of energy for all cells?
10. Why is the liver of such great importance in nutrition?
11. What is deamination?
12. Name the minerals most essential to the body, and tell what purpose each serves.
13. What are vitamins? State diseases which may result from vitamin deficiencies, and tell which vitamin cures each condition. What vitamins are found in milk? eggs? green vegetables? steak?
14. Utilizing the data of Table 7, plan a day's diet which would contain 3000 Calories and the necessary amounts of all required food factors. In what ways would the proper diets for a pregnant woman, a ten year old boy and a sixty-five year old man differ from this?

SUPPLEMENTARY READINGS

Sherman, H. C., and Lanford, C. S.: *Essentials of Nutrition*. 2d ed. New York, The Macmillan Company, 1943.
An elementary, well-written discussion of nutrition; one of the standard texts.

Youmans, J. B.: *Nutritional Deficiencies*. 2d ed. Philadelphia, J. B. Lippincott Company, 1943.
A discussion of the results of the lack of vitamins.

CHAPTER 13

THE EXCRETORY SYSTEM

DURING the metabolic processes whereby the cells utilize, for energy and repair, the food brought to them by the blood stream, certain waste products are formed which must be eliminated along with wastes resulting from the wearing out of protoplasm itself. These wastes are often toxic as well as useless and, if allowed to accumulate in the cells (as in certain types of kidney disease), will result in the death of the organism. The metabolic wastes which every cell of the body is constantly throwing off into the blood are eliminated continuously by the kidneys so that the concentration in the blood does not reach toxic levels.

It is important to keep in mind the distinction between **defecation, excretion,** and **secretion,** terms which are sometimes confused. Defecation refers to the elimination of wastes and undigested food, collectively called feces, from the anus. Undigested food never enters any of the body cells and so cannot take part in cellular metabolism; hence these are not metabolic wastes. Excretion refers to the removal of waste products (substances which have no further use in the body) from the cells and the blood stream into the urine and perspiration. The excretion of wastes by the kidneys involves an expenditure of energy by the cells, but the act of defecation requires no such effort of the cells lining the intestine. Secretion is the giving off by a cell of some substance that is used in a certain body process—for example, the salivary glands secrete saliva, used in the mouth and stomach for digestion. Secretion also involves cellular activity and requires the expenditure of energy by the secreting cell.

The excretory system of the human body involves more than just the kidneys and their ducts; the skin, lungs and digestive tract have excretory functions too. We have discussed previously the elimination of carbon dioxide, one of the most important metabolic wastes, by the lungs; the excretion of bile pigments, the breakdown products of hemoglobin, by the liver; and the excretion of certain metals, such as calcium, by the colon. The sweat glands of the skin are primarily concerned in the regulation of body temperature, but they also serve the purpose of excreting 5 to 10 per cent of all metabolic wastes. Sweat contains the same substances (salts, urea and other organic compounds) as urine, but is much more dilute, having only about one eighth as much solid matter. The volume of perspiration varies from about 500 cc. on a cool day to as much as 2 or 3 liters on a hot one. From tests made by the Army during World War II, it was found that, while doing a maximum of work at high temperatures, some men would excrete from 3 to 4 liters of sweat in an hour!

I. THE KIDNEY AND ITS DUCTS

Although the kidneys are the most important excretory organs of mammals, performing approximately 75 per cent of the work of excretion, they are important for other functions as well. They regulate the concentration of various substances dissolved in the blood, maintaining the balance between acids and alkalis, and keep the blood volume constant. Since the concentration of substances in all body fluids is determined largely by their concentration in the blood, the kidneys indirectly regulate the composition of all body fluids.

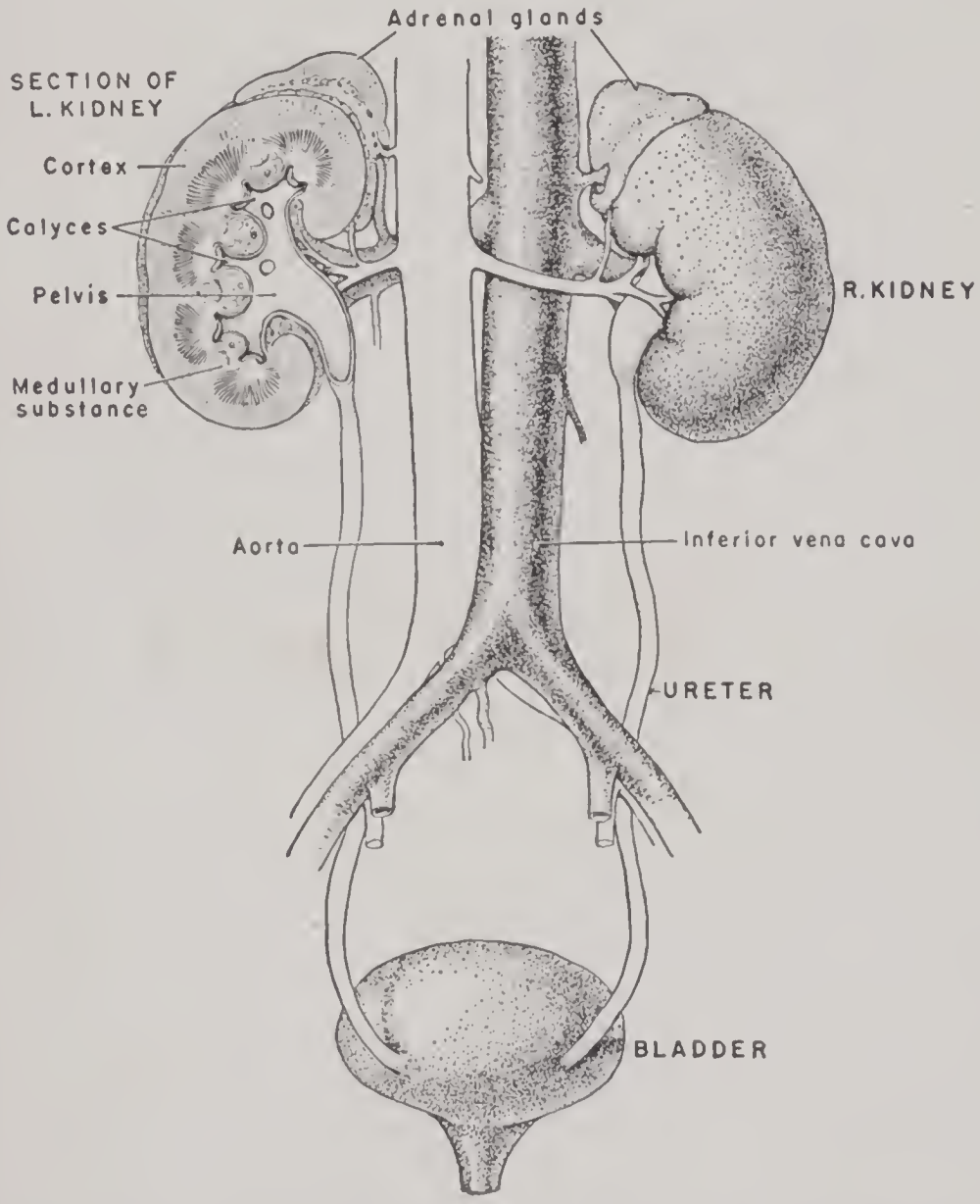


Fig. 112. The human urinary system, seen from the back or dorsal side. The left kidney is cut open to reveal the internal structures. (Hunter and Hunter: College Zoology.)

The kidneys are a pair of bean-shaped structures about 4 inches long, one of which is located on each side of the mid-dorsal line of the abdominal cavity, just below the level of the stomach (Fig. 112). On the medial, concave side of each kidney is a funnel-shaped chamber called the **pelvis**.* The urine, excreted by the kidney in a continuous trickle, collects in the pelvis and passes down the **ureters** by peristaltic waves

* Not to be confused with the pelvic bone, or pelvis, of the skeleton.

of contraction of the ureter walls to the **urinary bladder,** a hollow, muscular organ located in the lower, ventral part of the abdominal cavity (Fig. 112). The muscular walls of the bladder relax and distend to make room for it as it accumulates. Valves at the openings of the ureters into the urinary bladder prevent the backflow of urine, and keep any bacteria which may be in the bladder from ascending to the kidney. As the volume of urine in the bladder increases, the distention of the muscular walls stimulates nerve endings located there to send impulses to the brain, producing the sensation of fullness. To make urination possible, impulses originating in the brain cause a contraction of the bladder and a relaxation of the sphincter guarding the opening from the bladder to the urethra.

Upon dissection, the kidney is found to consist of masses of tubules arranged in an inner core, the **medulla,** and an outer layer, the **cortex.** Holding the tubules together is a fine network of connective tissue fibers; in addition, the tubules are richly supplied with blood vessels. Each tubule excretes a small part of the daily urine output of the whole kidney. The waste products brought to the kidney from cells all over the body by the blood stream must be removed from the blood and excreted as urine, without loss from the blood of any of the substances which the body needs. Blood enters the kidney by a branch of the dorsal aorta, the kidney artery, which ramifies to all parts of the organ; ultimately each final branch or arteriole goes to the end of each kidney tubule. There it branches into a spherical tuft of capillaries, called a **glomerulus** (Fig. 113). The end of each kidney tubule is a double-walled hollow sac of cells, called **Bowman's capsule,** which surrounds the glomerulus. The inner wall of Bowman's capsule consists of flat epithelial cells which adhere closely to the capillaries of the glomerulus, so that substances may diffuse easily from the capillaries into the cavity of Bowman's capsule.

1. The Formation of Urine. The formation of urine is a complex process, consisting of three parts: **filtration, reabsorption,** and **augmentation.** Filtration occurs at the junction between the glomerular capillaries and the wall of Bowman's capsule; the blood is "filtered" as it passes through the capillaries so that water, salts, sugar, urea and all the substances in the blood, except the plasma proteins and the blood cells, pass across this junction into the cavity of Bowman's capsule to become the **capsular filtrate.** The blood going through the glomerulus loses only about 1 per cent of its volume to the capsular filtrate, the rest passing from the glomerulus in the outgoing blood vessel. The mechanism underlying this process is the purely physical one of filtration, and depends on the fact that the small artery entering the glomerulus is larger than the vessel leaving it. Consequently the blood pressure in the glomerular capillaries is relatively high, and causes a small fraction of the blood to filter across into the capsule. By introducing a fine glass syringe into the Bowman's capsule of a frog's kidney and actually collecting and analyzing some of the capsular filtrate, Dr. A. N. Richards of the University of Pennsylvania showed that it has the same concentration of urea, salts, glucose, and so forth, as the plasma, but lacks its proteins. The cells of Bowman's capsule are thin and un-

able to move materials from the capillaries; the work of pushing the filtrate from the plasma into the capsule is done by the heart. It can be shown experimentally that as the blood pressure, and consequently the filtration pressure, rise and fall, the quantity of capsular filtrate varies accordingly.

If the composition of the urine excreted were like that of the capsular filtrate, excretion would be a wasteful process, and a great deal of

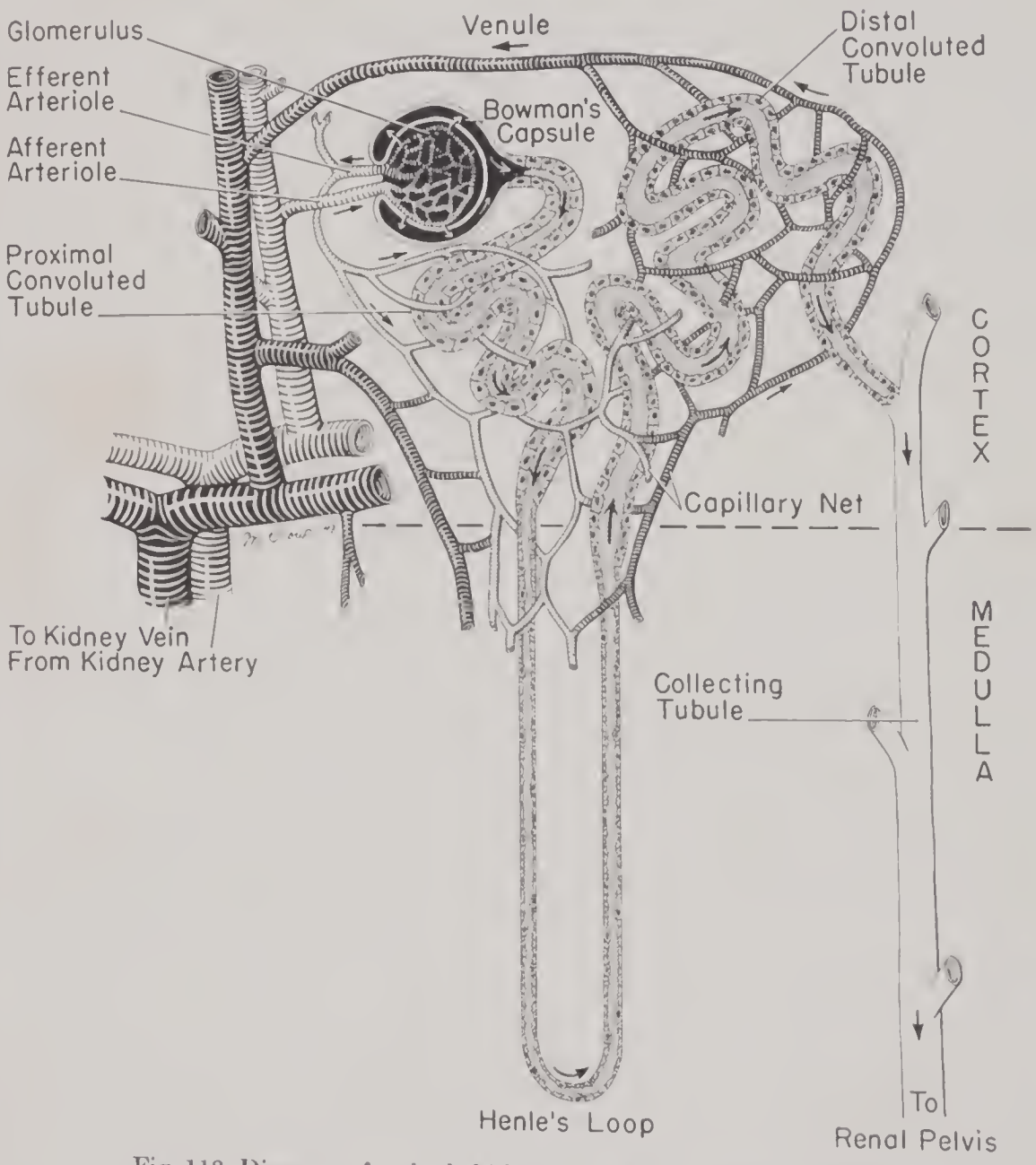


Fig. 113. Diagram of a single kidney tubule and its blood vessels.

water, glucose, amino acids and other useful substances would be lost. However, the kind and quantity of substances present in the urine are quite different from those in the plasma and capsular filtrate. From each Bowman's capsule, located in the cortex, the filtrate passes first through a proximal convoluted region of the tubule (also in the cortex) then through a long loop going into the medulla and back into the cortex, then through a second region in the cortex, the distal convoluted tubule, to empty at last into a collecting tubule, through which it passes to the pelvis (Fig. 113). There is no later change in the urine as it passes from the pelvis of the kidney through the ureters, bladder and urethra; the

changes in concentration occur when the materials pass from the Bowman's capsules through the long coiled tubules to the collecting tubule.

The walls of the kidney tubules are made of a single layer of flat or cuboidal epithelial cells, which, as the filtrate passes through, remove or reabsorb much of the water and virtually all the glucose, amino acids and other substances needed by the body, and secrete them back into the blood stream. This is possible because the blood vessel leaving the glomerulus does not go directly to a vein, but connects with a second network of capillaries around the proximal and distal convoluted tubules (Fig. 113). Thus the route of blood in the kidney differs from that in every other organ—for blood to pass from a kidney artery to a kidney vein, it must pass through two sets of capillaries; the ability of the kidney to excrete urine and regulate the composition of the blood depends upon this fact. Substances are reabsorbed into the blood stream selectively, according to the momentary needs of the body; if there is already too much glucose in the blood, as in a patient suffering from diabetes glucose is not reabsorbed, but passes on in the urine. The cells lining the tubules must do work to secrete these substances back into the blood stream, usually against a diffusion gradient. In fact, a given amount of kidney tissue consumes a larger amount of oxygen per hour than an equivalent weight of heart muscle, indicating that the kidney works harder than the heart. They obtain the energy for this work from the oxidation of carbohydrates; when the kidney is deprived of oxygen, reabsorption (though not filtration) ceases.

The human kidney produces about 100 liters of filtrate for every liter of urine formed; the other 99 liters of water are reabsorbed. In this way the waste products, such as urea, are greatly concentrated as the filtrate passes down the tubules. The concentration of urea in the urine is about sixty-five times that in the capsular filtrate and would be even higher but for the fact that a small amount of urea is reabsorbed by the tubules. The quantity of water reabsorbed depends also on the body's current needs for it. If a large quantity of water or beer is drunk, less water is reabsorbed and a copious, dilute urine is excreted. If water intake is restricted, a maximum amount of water is reabsorbed by the cells of the tubules, conserving water for the body, and a scanty but concentrated urine is excreted.

The cells of the kidney tubules not only remove substances from the filtrate and put them back into the blood stream, but also excrete additional waste material from the blood stream into the filtrate. This process, called **augmentation**, probably plays only a minor role in human kidney function, but in animals like the toadfish, whose kidneys lack glomeruli and Bowman's capsules, excretion by the tubules is the only method used. When the blood pressure, and consequently the filtration pressure, drop below a certain point, filtration ceases in man, although urine is still formed by tubular excretion. Dyes injected into experimental animals can be seen to pass from the blood stream into the urine through the cells lining the tubules. There is no doubt, then, that augmentation can occur in man and other animals, but just how large a role it normally plays in the process of excretion is unknown.

By the time the fluid reaches the end of the distal convoluted tubule.

and some substances have been reabsorbed and others added, the capsular filtrate has become urine.

2. The Regulatory Function of the Kidney. By the selective excretion of certain substances and the reabsorption of others, the kidney plays an extremely important role in regulating the composition of the blood and other body fluids. Any excess of acid or alkali released during metabolism is excreted by the kidneys, thereby maintaining the proper *p*H of the blood. By the same process the kidneys regulate the osmotic pressure of the body fluids bathing the cells, by regulating the concentration of salts in the blood. This is important, because if the concentration of salts in the body fluids exceeds that within the cells, water passes out of the cells and they shrivel and die. Or if the concentration of salts in the body fluids falls below that within the cells, water passes into the cells, causing them to swell and burst.

Although there is glucose in the capsular filtrate, there normally is none in the urine because it is reabsorbed by the cells of the tubules. But if there is so much glucose present in the blood, and consequently in the capsular filtrate (as there is in diabetics) that not all of it can be reabsorbed in the time the filtrate passes through the tubules, some glucose will appear in the urine. When the concentration of glucose in the blood reaches this point, it is said to have reached the "kidney threshold," which, for glucose, is about 150 mg. per 100 cc. of blood. Many other substances have "kidney thresholds," but the concentration at which the substance begins to appear in the urine is different for them.

The kidney regulates the total volume of blood as well as the concentration of the substances dissolved in it. When the total amount of blood is decreased, as, for example, after a hemorrhage, the blood pressure is lessened, and since the filtration pressure depends on the blood pressure, it is decreased correspondingly so that less liquid is filtered through the glomeruli into the Bowman's capsules. Hence the kidney produces a smaller volume of urine, and body fluids are conserved. When a great deal of liquid is taken in, the blood volume, blood pressure and filtration pressure are raised, resulting in a larger volume of urine, which restores the normal balance.

The quantity of urine excreted depends not only on how much liquid is consumed, but also on the concentration of salts and other solids to be excreted from the blood. When food is unusually salty, the kidney must excrete a proportionately large amount of salt to maintain the proper osmotic pressure of the blood, and the urine volume is increased. Since the solids excreted are dissolved in the urine, an increased amount requires more water to pass them. That is why **diabetes,*** of which one of the chief symptoms is the presence of sugar in the urine, is also characterized by a copious flow of urine. An increased amount of dissolved solids in the capsular filtrate increases its osmotic pressure and consequently decreases the rate of reabsorption of water, resulting in the increase in urine volume. This mechanism enables the kidney to respond

* The word "diabetes" simply means "to go through." In diabetes mellitus (mellitus means sweet, indicating the presence of sugar) a pathological condition of the pancreas lowers the amount of insulin formed, resulting in impaired carbohydrate metabolism and increasing the concentration of glucose in the blood and urine.

to increases in the concentration of urea and other wastes in the blood, since the higher concentration itself stimulates the flow of urine and the excretion of wastes.

Another factor controlling the urine volume is a hormone produced by the posterior lobe of the pituitary (p. 320) which controls the rate at which water is reabsorbed by the kidney tubules. In a comparatively rare disease, **diabetes insipidus** (insipid indicating a lack of sugar), due to a deficiency or complete lack of this hormone, the output of urine may reach 30 or 40 liters per day instead of the normal 1.2 to 1.5 liters, and the patient suffers from an insatiable thirst.

3. Substances Present in the Urine. Since the kidneys excrete, in addition to the normal products of metabolism, most of the abnormal substances that may enter or be formed in the body, analyzing the urine is a reliable method for determining the general metabolic condition of the body. Normal urine is about 96 per cent water, 1.5 per cent salts, and 2.5 per cent organic wastes, chiefly urea. The salts in the urine are the same as those in the blood and protoplasm, chiefly sodium chloride, with small amounts of potassium, calcium, magnesium and ammonium sulfate, phosphate and carbonate.

Of the 1200 to 1500 cc. of urine excreted daily, about 60 gm. are solids; half of this is made up of **urea,** which comes from the deamination of proteins. Both the nucleus and cytoplasm of all cells contain a modified protein known as nucleoprotein; **uric acid** is the breakdown product of this, and is another normal constituent of urine. Still another important organic waste product found in the urine is **creatine,** which comes from muscle metabolism.

The yellow color of urine is not due to any of the substances mentioned, but depends on the presence of a pigment called **urochrome,** a breakdown product of hemoglobin related to the bile pigments.

4. Diseases of the Kidneys. A painful and often fatal disease, **nephritis,** is caused by the presence of bacteria in the kidneys, which infect the cells. They usually attack the glomeruli, causing them to become more permeable than normal, so that proteins and even intact blood cells pass through into the urine. Because of the constant loss of proteins from the blood, the ability of the plasma to reabsorb water from the tissue fluid around the capillaries is lowered, and a watery swelling, known as **edema,** occurs, especially in the lower parts of the legs. In the last stages of this disease there is a marked decrease in the amount of urine formed, and the waste products normally excreted by the kidneys accumulate in the blood (a condition called uremia). Because some of these substances are toxic, death occurs unless the condition is relieved immediately.

Impairment of the kidneys is often associated with high blood pressure, because the abnormal pressure tends to injure the glomeruli, and the decreased supply of blood to the kidney cells, resulting from the constriction of the arteries, may cause damage. Recent experiments have shown that injured kidneys give off a substance called **renin,** which causes constriction of the blood vessels, thus raising the blood pressure and completing the vicious cycle.

Some of the solids normally present in the urine, uric acid and calcium

phosphate, are not very soluble, and when the amount present in the urine is increased, they may be precipitated in the urinary passages as "kidney stones." If these become large enough to block the passage of urine, they must be removed surgically, since once they form, it is impossible to redissolve them.

II. EXCRETORY DEVICES IN OTHER ANIMALS

Every organism has had to solve the problem of getting rid of metabolic wastes. In protozoa, such as amebas and paramecia, the wastes simply diffuse through the cell wall into the outside environment where the concentration is lower. Protozoa living in fresh water have a special problem in getting rid of water, because their protoplasm, being hypertonic to pond water, tends to absorb it continuously. To control this situation, which would otherwise result in a swelling and bursting of the cell, they have a contractile vacuole, a small vesicle in the proto-

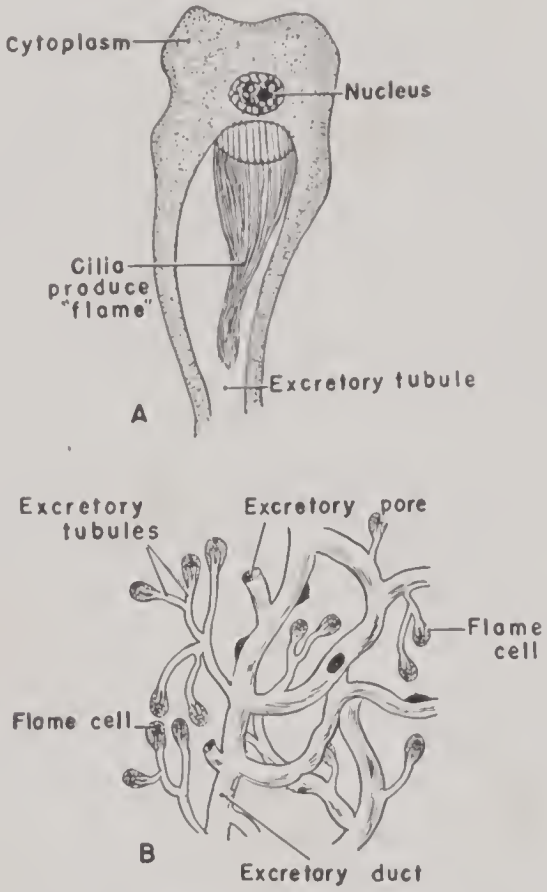


Fig. 114. *A,* Flame cell, much enlarged, from a planarian. *B,* Diagram illustrating the arrangement of flame cells and collecting ducts of the excretory organ of the planarian. (Hunter and Hunter: College Zoology.)

plasm which empties water from the interior of the cell as fast as it is taken in. Hydras and other coelenterates also have direct excretion of wastes by diffusion through the cell membrane.

In larger animals the elimination of wastes by diffusion is not adequate to prevent toxic accumulations, and various excretory devices are necessary. In flatworms there are specialized hollow tubes called **flame cells** (Fig. 114), composed of cells opening to the exterior which have a tuft of cilia at the interior end. Wastes from all other cells diffuse into these tubes and are expelled by the beating of the cilia. This beating resembles the flickering of candlelight; hence the name.

Earthworms have in each segment of their bodies a pair of specialized organs, called **nephridia,** which function in excretion. Each nephridium is a long coiled tubule (Fig. 115), opening at one end into the body cavity and at the other end to the exterior. Around each tubule is a coil of capillaries, which permits the removal of wastes from the blood stream. The internal end of the nephridium is funnel-shaped and supplied with beating cilia which set up a current to move the body fluid into the organ. As the body fluid passes through, water and substances such as glucose are reabsorbed, while the wastes are concentrated and passed out of the body.

The excretory system of insects consists of organs called **malpighian tubules,** which lie within the body cavity and empty into the digestive

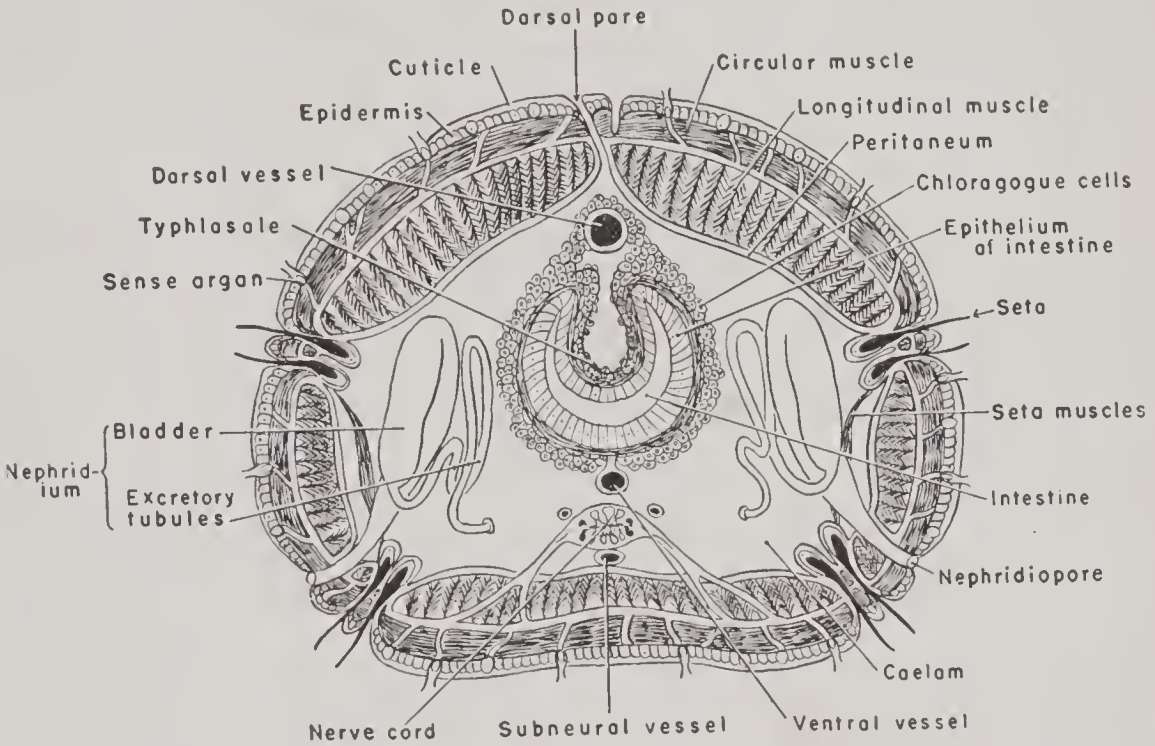


Fig. 115. Cross section of the common earthworm, *Lumbricus terrestris,* showing the excretory organs, the paired nephridia. Each consists of a ciliated funnel opening into the celomic cavity, a coiled tubule, and a pore opening to the outside. (Hunter and Hunter: College Zoology.)

tract. Waste products from the body cavity diffuse into these tubules and are excreted into the digestive tract, whence they are carried to the exterior with the undigested food.

The urinary systems of all the vertebrates are essentially the same. In the lower vertebrates the kidney tubules open into the body cavity instead of into Bowman's capsules, and thus represent a type of excretory organ intermediate between the nephridia found in the earthworm and the kidneys of higher vertebrates. The evolution of the urinary system is complicated by the fact that in many animals the reproductive system has come to share some of the structures of the urinary system, so that various organs play a dual role. This relationship is so close that the two systems are frequently considered together as the "urogenital" system.

III. EXCRETION IN PLANTS

A striking difference between plants and animals is that plants excrete little or no nitrogenous wastes. Those excreted by animals—urea, uric acid and ammonia—come from the breakdown of proteins and other substances. Similar nitrogenous compounds are released during the metabolism of plant protoplasm, but instead of being excreted as wastes, they are reutilized in the synthesis of new protoplasm. Since plants neither ingest proteins nor carry on muscular activity (the two largest sources of metabolic wastes in animals), the total amount of nitrogenous waste is small and can be eliminated by diffusion as ammonia through the pores of the leaves, or by diffusion as nitrogen-containing salts from the roots into the soil. In some plants a few waste products accumulate and remain as crystals within the cells; for example, spinach leaves contain about 1 per cent oxalic acid.

QUESTIONS

1. What is the difference between excretion and defecation?
2. Name the organs which perform excretory functions in man.
3. Explain in detail how metabolic wastes are eliminated from the body via the kidney.
4. How do the kidneys regulate the osmotic pressure of the body fluids?
5. What does the term "kidney threshold" mean?
6. What is the composition of urine?
7. What are kidney stones, and how are they formed?
8. How is excretion accomplished in one-celled animals?
9. Explain how the nephridia of earthworms carry on the excretory process.
10. What happens to the metabolic waste products of plants?

SUPPLEMENTARY READINGS

Best, C. H., and Taylor, N. B.: *The Living Body*. New York, Henry Holt & Company, Inc., 1944.
A clear, understandable presentation of human physiology.

Carlson, A. J., and Johnson, V.: *The Machinery of the Body*. 3rd ed. Chicago, University of Chicago Press, 1948.
A well-written and illustrated discussion, on a fairly simple level, of human physiology.

Fulton, J. F.: *Howell's Physiology*. 16th ed. Philadelphia, W. B. Saunders Company, 1949.
One of the standard, detailed, advanced texts of physiology.

Gerard, R. W.: *The Body Functions*. New York, John Wiley & Sons, Inc., 1941.
An interesting account of circulation, digestion and excretion in man.

Millard, N. D., and King, J. B.: *Human Anatomy and Physiology*. 2d ed. Philadelphia, W. B. Saunders Company, 1945.
A good, clear presentation, on an elementary level, of the excretory process in man.

Rogers, C. G.: *Textbook of Comparative Physiology*. New York, McGraw-Hill Book Company, Inc., 1938.
Contains a discussion of the excretory processes of many different types of animals.

CHAPTER 14

THE INTEGUMENTARY AND SKELETAL SYSTEMS

ACCORDING to our earlier definition, an organ system is a group of organs, related in function, which operate together to perform a specific and necessary task for the maintenance of life. The skin, which covers the body, and the bony framework which supports it, are both organ systems, although they may not seem to be so on first consideration. The integumentary and skeletal systems function independently of each other, but since both act as protective devices for the body, and because together (with the muscles) they determine the shape and symmetry of the body, we shall consider them in the same chapter.

I. THE SKIN

All multicellular animals are covered externally by a skin or **integument,** consisting of one or many layers of cells. The skin is much more than merely an outer wrapping for the animal; it is one of the important body organs and performs many diverse functions. Perhaps the most obvious and vital of these is to protect the body against a variety of external agents. Being tough and pliable, it shields the underlying cells from mechanical injuries caused by pressure, friction or blows. Since it is practically germproof as long as there is no break in it, the skin also protects the body against disease-producing organisms. Its waterproof quality protects the body from excessive loss of moisture, or, in aquatic animals, from the excessive intake of water. Important, too, is the protection it affords the underlying cells from the harmful ultraviolet rays of the sun, by virtue of the pigment it can produce (sun tan).

Another necessary function of the skin is that of a thermostatically controlled radiator, which regulates the elimination of heat from the body. Since heat is constantly being produced by the metabolic processes of the cells and distributed by the blood stream, a certain amount of heat must be lost all the time to maintain a constant temperature within the body. Some heat leaves the body in the expired breath and some in the feces and urine, but approximately 90 per cent of the total lost is given off by the skin. When the external temperature is low, temperature-sensitive nerve endings in the skin are stimulated, and the capillaries in the skin are reflexly contracted, thereby decreasing the flow of blood through the skin and the rate of heat loss. In a warm environment the reverse occurs: the capillaries expand, and the increased flow of blood causes the skin to appear flushed and results in an increased heat loss. In very warm environments this mechanism is not sufficient to get rid of the necessary amount of heat, so that the sweat glands of

the skin give off an unusually great amount of perspiration. The evaporation of sweat from the surface of the skin lowers the body temperature by removing from the body the heat necessary to convert the liquid sweat into water vapor—540 Calories are required to convert a liter of water to water vapor.

The skin is also important in containing a number of different sense receptors which are responsible for our ability to feel pressure, temperature and pain, and to discriminate between the various objects touched In addition, specialized glands are located in the skin: some 2½ million sweat glands occur all over the body, but are most numerous on the palms of the hands, the soles of the feet, in the arm pits and on the forehead; oil glands, too, are found all over the body, but are especially numerous on the face and scalp. They secrete a film of oil to keep the

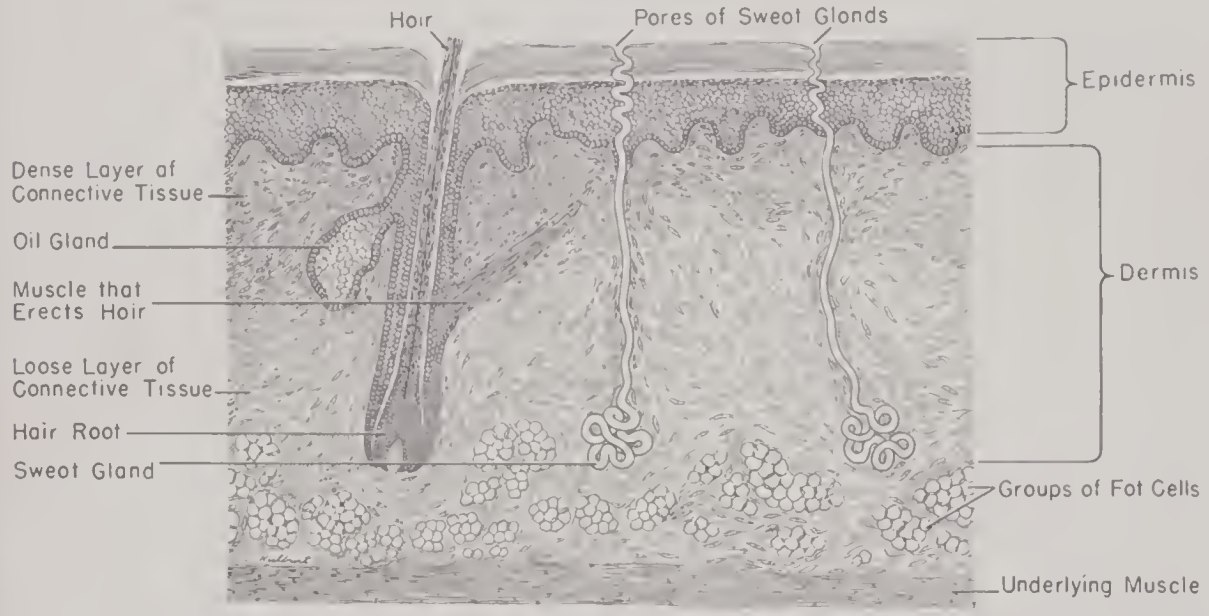


Fig. 116. Microscopic section through the human skin, showing dermis, epidermis, hair, and oil and sweat glands.

hair moist and pliable and to prevent the skin from drying and cracking. The mammary glands of mammals are also derivitives of the skin, specialized for the secretion of milk.

1. Parts of the Skin. The skin is composed of two main parts: a comparatively thin, outer layer, the **epidermis,** free of blood vessels; and an inner, thicker layer, the **dermis,** packed with blood vessels and nerve endings (Fig. 116). Although we speak of the epidermis as one layer, it is really made up of several layers of different kinds of cells, which vary in number in different parts of the body. Thus, the thickness of the skin is not everywhere the same; it is thickest on the soles of the feet and the palms of the hand, where the epidermal surface is thrown into countless tiny ridges which form the fingerprint patterns. These patterns are unique in each person and remain constant throughout life. The layer of the epidermis lying next to the dermis is made up of columnar cells which undergo frequent cell division to give rise to the layers above. The outer layers of the skin are constantly sloughing off and being replaced in this way. As each cell is pushed outward from the bottom layer, it is compressed into a flat epithelial cell, which is lifeless

and scalelike. Dandruff consists of the flaky particles of dead, outer epidermal cells of the scalp.

The dermis is much thicker than the epidermis and is composed largely of connective tissue fibers and cells. The outer part, made of thickly matted connective tissue fibers, is the portion which is tanned to make leather. Below this, and connected with the underlying muscles, is a layer composed of many fat cells and a more loosely woven network of fibers. This part of the dermis is one of the principal depots of body fat; because of its location, the fat also helps prevent excessive loss of heat and acts as a cushion against mechanical injury. The dermis is richly supplied with blood and lymph vessels, nerves, sense organs, sweat glands, oil glands and hair follicles.

The color of the skin depends on three factors: the yellowish tinge of the epidermal cells, their translucent quality which allows the pink of the underlying blood vessels to show through, and the kind and amount of pigment—red, yellow or brown—contained in the inner layer of epidermal cells.

2. Outgrowths of the Skin. The hair and nails of man and the feathers, scales and horns of other animals are derivatives of the skin. The entire skin, except the palms of the hands and soles of the feet, is equipped with countless hair follicles—inpocketings of cells from the inner layer of the epidermis. These cells undergo division and give rise to the hair cells, just as the inner layer of the epidermis gives rise to the outer layers. But the hair cells die while still in the follicle, and the hair visible above the surface of the skin consists of tightly packed masses of their remains. Hair, then, grows from the bottom of the follicle, not from the tip. Its color, and that of feathers and fur (which is a form of hair), depend on the amount and kind of pigment present, on the number of air bubbles, and on the nature of the surface of the hair, which may be smooth or rough.

Fingernails and toenails also develop from inpocketings of cells from the inner layer of the epidermis, and the growth of nails is similar to that of the hair. Nails are composed of densely packed dead cells which are translucent, allowing the underlying capillaries to show through and giving the nails their normal pink color.

Oil and sweat glands are derived from the inner layer of the epidermis by inpocketings which go deep into the dermis. Each hair follicle is associated with an oil gland.

II. THE SKELETON

The first and most obvious function of the skeleton is to give support and "shape" to the body. In order that an animal may rise off the ground and move around, some hard, durable substance is needed to maintain the soft tissues against the pull of gravity and act as a firm base for the attachment of muscles. These requirements are met by the bones. The skeleton also protects the delicate underlying organs, such as the brain and lungs, from injury. The marrow tissue, within the cavity of the bones, performs the special task of manufacturing all red corpuscles and some kinds of white ones.

The skeletal system is not made up of bones only; connective tissue

fibers are an important part of it, too, helping to maintain body form by holding the organs together. Two specialized kinds of connective tissue fibers, ligaments and tendons, attach bones to bones, and muscles to bones, respectively, thereby playing an indispensable role in locomotion.

3. Types of Skeletons. The skeleton of an animal may be located on the outside of the body (an **exoskeleton**) or inside the body (an **endoskeleton**). The hard shells of lobsters and crabs, and the shells of oysters, clams and snails, are examples of exoskeletons. The advantage of an exoskeleton as a protective device is obvious, but a serious disadvantage is the attendant difficulty of growth. Snails and clams meet the

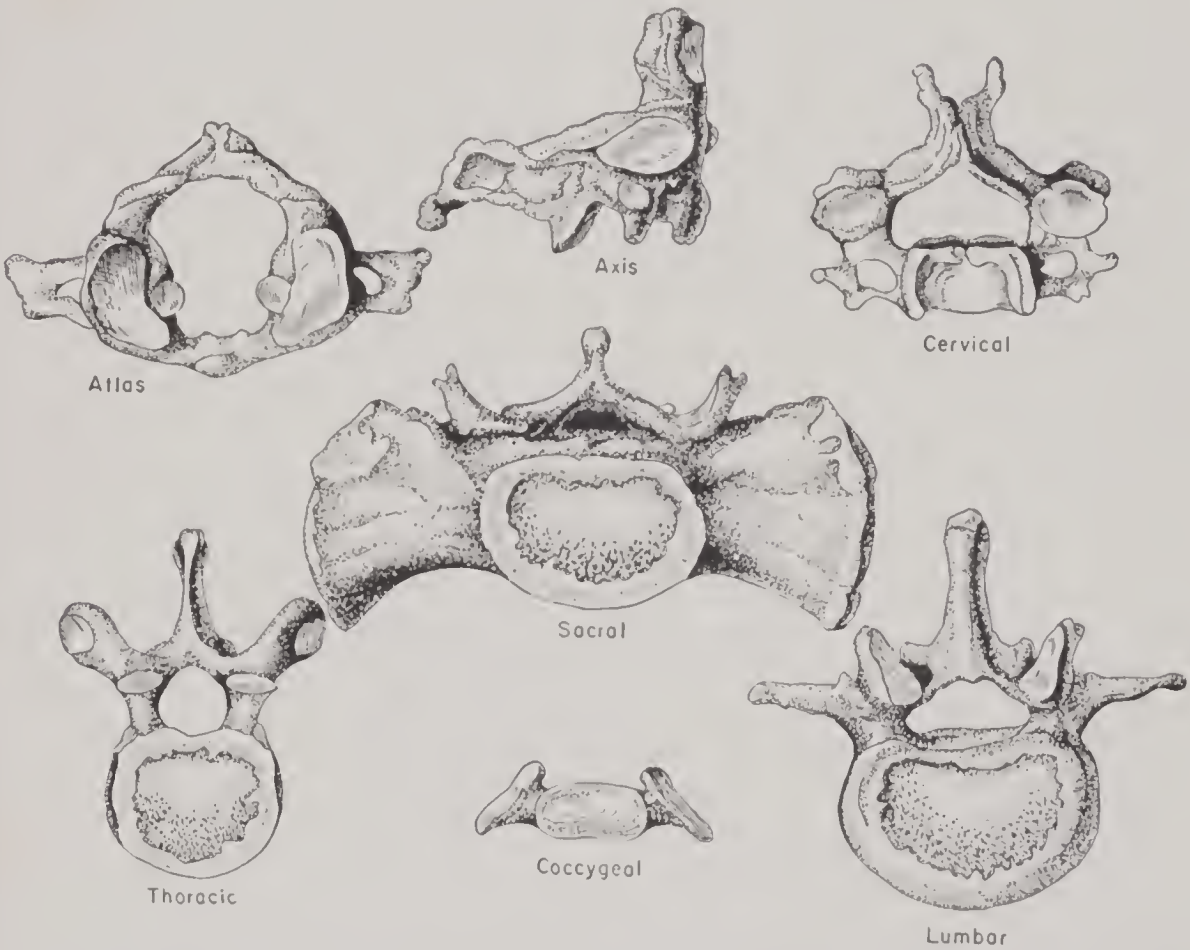


Fig. 117. Different types of human vertebras. The axis is shown in side view; all others are seen from above. (Hunter and Hunter: College Zoology.)

difficulty by secreting additions to their shells as they grow, and lobsters and crabs have evolved a complicated solution whereby the outer shell is first softened by the removal of some of its salts, enabling it to be split down the back. The animal then crawls out of the old shell, grows rapidly for a short time, and produces a new, larger shell which hardens by the redeposition of mineral salts. During this process the animal, being weak and barely able to move, easily falls prey to its enemies.

Man and all the other vertebrates have a characteristic endoskeleton. The skeleton of sharks and rays is made of cartilage, but in the higher fishes and other vertebrates most of the cartilage has been transformed to bone. The human skeleton consists of approximately 200 bones; the exact number varies at different periods of life, as some of the bones which at first are distinct, gradually become fused. Most of the bones

are hollow and contain the bone marrow cells, which manufacture red and white blood cells.

4. Parts of the Skeleton. For purposes of study the vertebrate skeleton may be divided into the **axial skeleton** (the bones and cartilages in the middle or axis of the body), and the **appendicular skeleton** (the bones and cartilages of the fins or limbs). The axial skeleton consists of the **skull, backbone** (vertebras), **ribs** and **breast bone** (sternum).

The skull is made up of a number of bones fused together: the **cranium** or bony case immediately around the brain, and the bones of the face. The lower vertebrates have gill arches, cartilages or bones supporting the gill pouches, but in the higher vertebrates these have disappeared or have been converted into other structures, such as the small bones in the middle ear—the hammer, anvil and stirrup—which transmit sound waves from the ear drum to the inner ear. Certain gill arches of fishes have been transformed, in the higher forms, to parts of the epiglottis and larynx.

The backbone is made of thirty-three separate **vertebras** which differ in size and shape at different points along the spine. A typical vertebra (Fig. 117) consists of a basal portion, the **centrum,** to which is attached, dorsally, a ring of bone, called the **neural arch,** which surrounds and protects the delicate spinal cord. Different vertebras have different projections for the attachment of ribs and muscles and for articulating (joining) with neighboring vertebras. The skull articulates with the first vertebra (called the atlas), which has rounded depressions on its upper surface into which fit two projections from the base of the skull.

The rib basket is composed of a series of flat bones which support the chest wall and keep it from collapsing as the diaphragm contracts. The ribs are attached dorsally to the vertebras, each pair of ribs being attached to a separate vertebra. Of the twelve pairs of ribs in man, the first seven are attached ventrally to the breastbone, the next three are attached indirectly by cartilages, and the last two have no attachments to the breast bone, and so are called "floating ribs."

The bones of the appendages, or arms and legs, and the **girdles** which attach them to the rest of the body, make up the appendicular skeleton. The **pelvic girdle** consists of three fused hip bones, and the **pectoral girdle** consists of the two collar bones, or **clavicles,** and the two shoulder blades, or **scapulas.** The pelvic girdle is securely fused to the vertebral column, while the pectoral girdle is loosely and flexibly attached to it by means of muscles. Both the pectoral and pelvic fins of fishes are simple structures, adapted for paddling. Paleontological evidence shows that such fins as these evolved into limbs adapted for moving on land, and that these in turn evolved into wings, hoofs, and the flippers of whales.

The appendages of man are comparatively primitive, terminating in five digits—the fingers and toes—whereas the more specialized appendages of other animals may be characterized by four digits (as in the pig), three (as in the rhinoceros), two (as in the camel), or one (as in the horse). The diagrams in Figure 118 illustrate the arrangement of the bones in the appendages.

The bones of the arm are the **humerus** of the upper arm, the **radius** and **ulna** of the lower arm, the eight tiny **carpals** of the wrist, the five

slender **metacarpals** of the palm, and the fourteen **phalanges,** or finger bones—two in the thumb and three in each finger. The leg bones are the **femur** in the thigh, the **tibia** and **fibula** in the shank, the seven **tarsals** in the ankle, the five **metatarsals** across the instep, and the fourteen **phalanges** in the toes. The great toe has only two phalanges, every other toe having three. The **patella** or knee cap is a separate bone

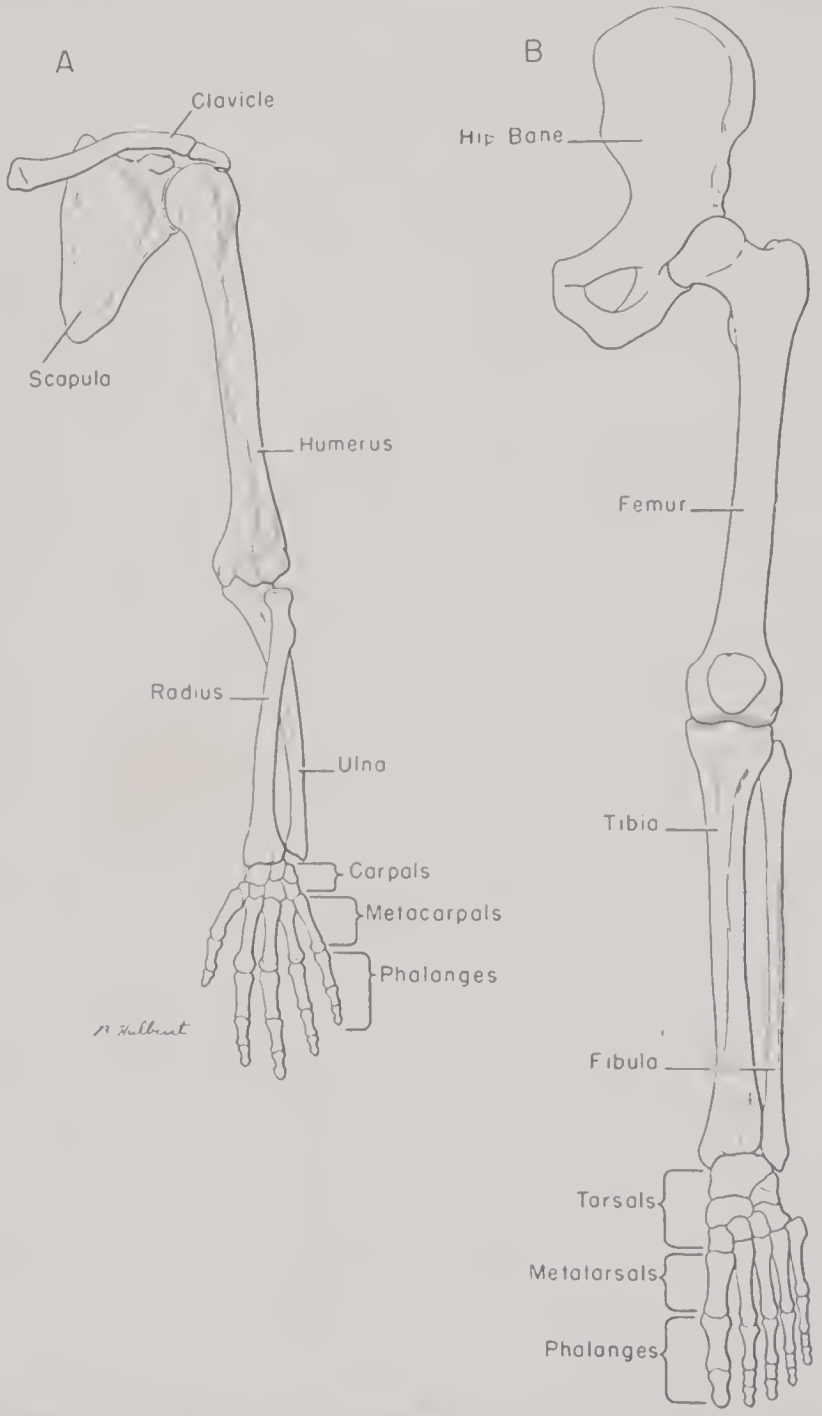


Fig. 118. Diagrams of the bones of the left arm (*A*) and left leg (*B*), as seen from the front. Note the fundamental similarity of pattern in the arrangement of the bones in the two limbs.

of the leg; there is no counterpart for it in the arm.

5. The Joints. The point of junction between two bones is called a **joint.** Some joints, such as those between the bones of the skull, are immovable and extremely strong, owing to an intricate dovetailing of the edges of the bones. Other joints, such as the articulation of the humerus to the scapula, or the femur to the hip bone, are in the form of a ball-and-socket, permitting free movement in several directions. Both the

scapula and hip bone contain rounded, concave depressions to accommodate the rounded, convex heads of the humerus and femur, respectively. Between these two extremes are joints with moderate freedom of motion, such as the hinge joint at the knee, which is restricted to movement in a single plane, or the pivot joints at the wrists and ankles, which are intermediate in freedom of movement between the hinge and the ball-and-socket types.

Wherever two bones move on one another, their ends do not touch directly, but are covered with smooth, slippery cartilage which reduces friction. The bearing surfaces are completely enclosed in a liquid-tight capsule made of ligaments, and the joint cavity is filled with a liquid, secreted by the membrane lining the cavity, which acts as a lubricant. This liquid is similar to lymph or tissue fluid, but contains a small amount of mucus. During youth and early maturity the lubricant is replaced as needed, but in middle and old age the supply is often decreased, with a resulting stiffness of joints and difficulty of movement.

6. Types of Locomotion. Animals differ as to the part of the foot they put on the ground in walking and running. Men and bears walk flat on the palm of the foot, a type of locomotion adapted for a comparatively slow gait, called **plantigrade.** To increase the effective limb length, and thus the running speed, some animals, such as dogs and cats, have become adapted to running on their digits, a type of locomotion called **digitigrade.** Speed is increased still further in the hoofed animals, horses and deer, by the lengthening of the limb bones and the raising of the wrist and ankle still further from the ground, so that the animal runs upon the tips of one or two digits of each limb. This is known as **unguligrade** locomotion, and the animals which have it are known as **ungulates.**

7. The Skeletal System of Plants. The supporting system of plants is quite different from that of animals, but land plants need a strong structure to hold the leaves in position to receive the sunlight necessary for photosynthesis. In place of the bones and cartilage of animals, large plants, such as trees and shrubs, have woody or xylem cells to support the leaves, stems and roots. These cells secrete a thick wall of cellulose impregnated with a complex chemical called **lignin,** which, to date, is unanalyzable. In addition, the phloem or inner bark of trees contains thick fibers to help support the trunk. Therefore, when these large plants are deprived of water and die, their trunks and branches remain upright.

Only trees and shrubs have a large central core of wood in the stem; the cell walls of smaller plants, such as tulips, grasses and wheat, contain no woody material. Their walls, being much thinner, depend on the turgor, or pressure of water within the cells, to support the stem, and when such plants are deprived of water they wilt and collapse.

QUESTIONS

1. What is the primary function of the skin? Name four other functions it performs.
2. Draw a diagram of a cross-section of the skin, labeling all the parts.
3. How is hair formed?
4. What three types of tissue are included in the skeletal system?
5. Differentiate between the axial and the appendicular skeleton. What is the difference between an exoskeleton and an endoskeleton? What vertebrates have an exoskeleton?

6. What are joints? Why do they become stiff in old age?
7. What are the supporting structures of trees and shrubs?
8. How are herbaceous plants supported?

SUPPLEMENTARY READING

Romer, A. S.: *The Vertebrate Body*. Philadelphia, W. B. Saunders Company, 1949.
A detailed, well-written comparison of the structures of the different types of vertebrates.

CHAPTER 15

THE MUSCULAR SYSTEM

IN MAN and most animals the ability to move depends upon a group of specialized contractile cells, the muscle fibers. In the vertebrates three different types of muscle fiber have evolved to perform various kinds of movements: **skeletal muscle,** which is attached to the bones of the skeleton; **cardiac** or heart muscle, which moves the blood through the circulatory system; and **smooth** muscle, which makes up the walls of the digestive tract and certain other internal organs, and moves material through the internal hollow organs. All three types of muscle have the ability to shorten when stimulated, and ordinarily this stimulation reaches the muscle fibers via a nerve. But both cardiac and smooth muscle can contract in the absence of nervous stimulation, and both the heart and the digestive tract function almost normally even when all the nerves leading to them have been cut. In contrast, when the nerves to skeletal muscle are severed or blocked, the muscle is completely paralyzed. For a few weeks it will respond to artificial stimulation, such as an electric shock applied to the overlying skin, but even this ability is gradually lost.

When the drug curare, the chief ingredient of the arrow poison of the South American Indians, is injected, it blocks the junction between nerve and muscle so that impulses can no longer pass. This produces the same effect as the cutting of the nerves to all the muscles of the body. The muscles of a curarized animal will still respond to direct electric stimulation, however, demonstrating that muscle is "independently irritable" and need not receive its stimulation through a nerve as it normally does.

A typical skeletal muscle is an elongated mass of tissue composed of millions of individual muscle fibers bound together by connective tissue fibers. The entire structure is surrounded by a tough, smooth sheet of connective tissue so that it can move over adjacent muscles and other structures with a minimum of friction. The two ends of the muscle are usually attached to two different bones, although a few muscles pass from a bone to the skin, or even, as in the case of the muscles of the face used in speech and expression, from one part of the skin to another. The end of the muscle which remains relatively fixed when the muscle contracts is known as the **origin;** the end that moves is called the **insertion;** and the thick part between the two is called the **belly** (Fig. 119). The origin of the biceps muscle of the upper arm is at the shoulder, and its insertion is on the radius bone of the forearm; when the biceps contracts, the shoulder remains fixed and the elbow is bent.

Muscles never contract singly, but always in groups. No matter how hard you try, you cannot contract the biceps muscle alone—you can

only bend the elbow, which involves the contraction of a number of other muscles besides the biceps. Further, muscles can exert only a pull, not a push. Hence they usually are paired as antagonists, one pulling a bone one way, another pulling it the opposite way. The names **flexor** and **extensor** are applied to muscles to indicate the type of movement they effect. Thus the biceps, which bends or flexes the arm, is called a flexor, and its opposing muscle, the triceps, with its origin on the shoulder and upper arm, and its insertion on the ulna, straightens or extends

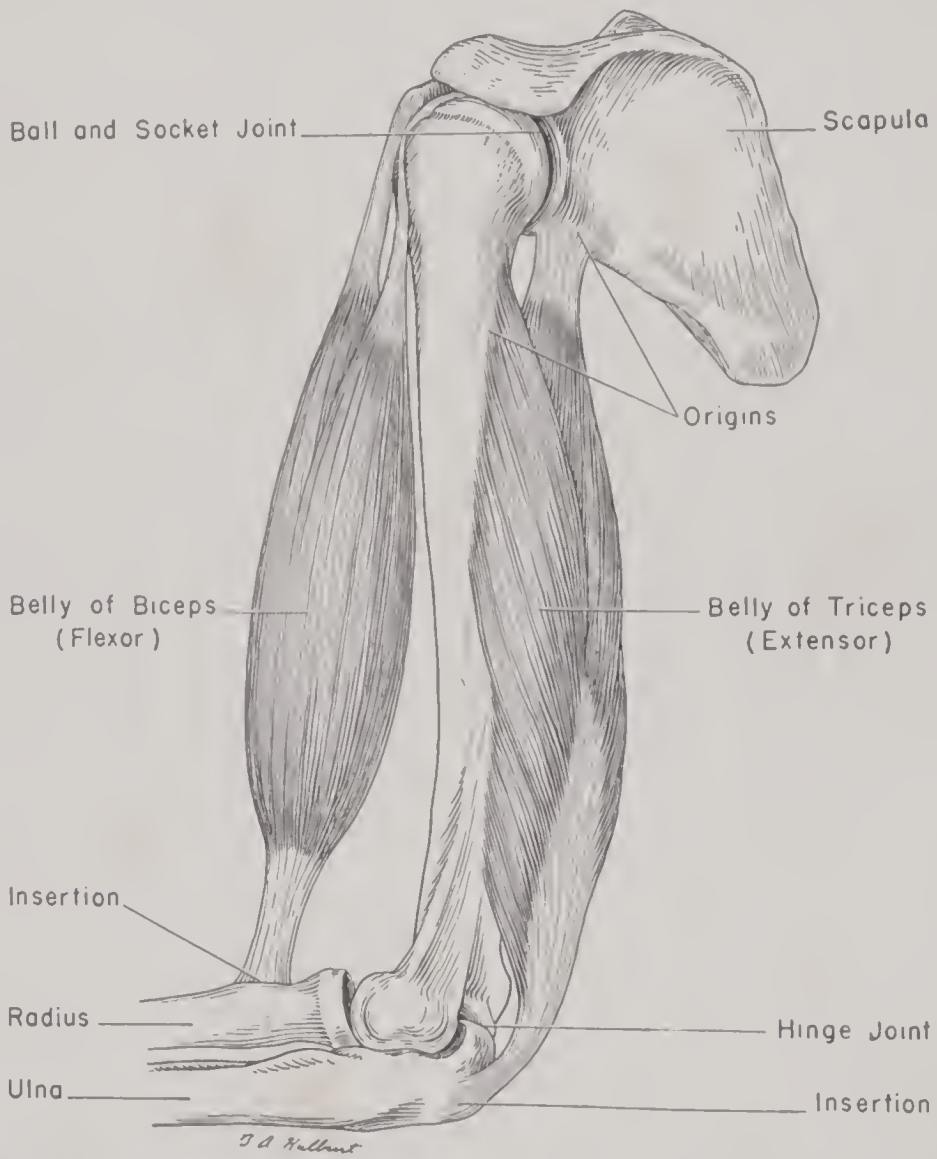


Fig. 119. Muscles and bones of the forearm, showing origin, insertion and belly of a muscle, and the antagonistic arrangement of the biceps and triceps.

the forearm and is called an extensor. Similar pairs of opposing flexors and extensors are found at the wrist, knee, ankle and other joints. Whenever a flexor contracts, the opposing extensor must relax to permit the bone to move, and this requires the proper coordination of the nerve impulses going to both sets of muscles.

When muscles are not contracting to effect a movement, they are not completely relaxed. As long as a person is conscious, all the muscles are contracted slightly, a phenomenon called tonus. Posture is maintained by the partial contraction of the muscles of the back and neck, and of the flexors and extensors of the legs. When a person is standing, both the flexors and extensors of the thigh must contract simultaneously so

that the body sways neither forward nor backward on the legs, and the simultaneous contraction of the flexors and extensors of the shank locks the knee in place and holds the leg rigid to support the body. When movement is added to posture, as in walking, a complex coordination of the contraction and relaxation of the leg muscles is required. It is not surprising that the process of learning to walk is long and tedious.

Some of the larger muscles of the body are extremely strong. Consider the muscle of the calf of the leg, called the **gastrocnemius,** which is used in rising on one's toes. Its origin is at the knee, and its insertion, by way of the tendon of Achilles, is on the heel bone; because the distance from the toes to the ankle joint is at least six times that from the ankle joint to the heel, the gastrocnemius is working against an adverse lever ratio of 6:1. This means that when a person weighing 150 pounds stands on one leg and rises on his toes, the one gastrocnemius muscle is exerting a force of 900 pounds; and if a man were to hold another person in his arms and perform this action, the muscle would be exerting a force of nearly a ton.

Because of nervous coordination, no normal person can cause his muscles to contract maximally, but in certain diseases in which the nervous control is absent, muscles do contract forcefully enough to rip tendons and break bones.

1. Kinds of Contraction. To understand how muscles contract, it is necessary to discriminate carefully between the contraction of a whole muscle and the contraction of its individual fibers. For although a muscle cannot contract maximally, a *single* fiber of it can respond *only* maximally, or not at all. This phenomenon, described as the "All or None Law," can be demonstrated experimentally by dissecting out a muscle fiber and giving it repeated stimuli of increasing intensity, beginning with ones too weak to cause contraction. As the strength of the stimulus is increased, there will be no response until a certain level is reached, at which time the fiber will contract completely. No stimuli of greater intensity can cause any greater contraction. Since a whole muscle is made up of thousands of individual muscle fibers, however, the nature and strength of *its* contraction depend upon the number of its constituent fibers which are contracting, and upon whether the fibers are contracting simultaneously or alternately.

In studying the different kinds of contraction, advantage is taken of the fact that a muscle will retain its ability to contract after it has been removed from the body. The muscle usually used for experimental purposes is the calf muscle of a frog, and if care is taken to keep it moist, it will contract for hours. To make a record of these contractions, the muscle is mounted with its origin attached to a fixed hook and its insertion connected, by means of another hook, to a lever with a pointed stylus at its tip. This stylus is in contact with a cylinder, covered with recording paper and revolved by clockwork, so that each contraction of the muscle raises the stylus and records its vigor and duration. Additional styluses can be used to record an appropriate time scale and to mark when the stimulus is given to the muscle.

The Single Twitch. When a muscle is given a single stimulus—for example, a single electric shock—it responds with a single, quick twitch.

which lasts about 0.1 second in a frog's muscle and about 0.05 second in a human muscle. Laboratory records of a single twitch (Fig. 120) indicate that it consists of three separate phases: (1) the **latent period,** lasting about 0.01 second, an interval between the application of the stimulus and the beginning of the visible shortening of the muscle; (2) the **contraction period,** about 0.04 second in duration, during which the muscle shortens and does work; and (3) the **relaxation period,** the longest of the three, lasting 0.05 second, during which the muscle returns to its original length. After a twitch the muscle consumes oxygen and gives off carbon dioxide and heat at a rate greater than during rest, indicating a **recovery period** in which the muscle is restored to its original condition. This recovery period lasts for several seconds, and if a muscle is stimulated repeatedly so that successive contractions occur before the muscle has recovered from the previous ones, the muscle becomes

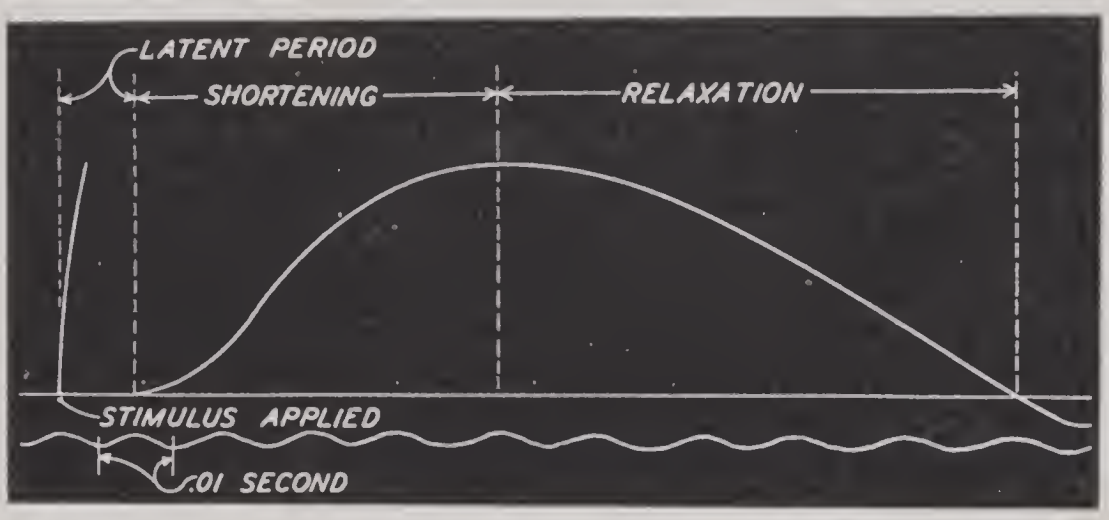


Fig. 120. The recording of a single twitch of a frog muscle made on a rapidly moving smoked plate, mounted on a kymograph. The wavy line at the bottom was made by a tuning fork vibrating 100 times a second. (Carlson and Johnson: The Machinery of the Body, published by University of Chicago Press.)

fatigued and the twitches grow feebler and finally stop. If the fatigued muscle is allowed to rest for a time, it regains its ability to contract.

Tetanus. The normal contractions of the muscles do not occur as single twitches, but as sustained contractions evoked by a volley of separate stimuli—the nerve impulses—reaching them in rapid succession. Such a sustained contraction is called **tetanus,*** and while it prevails, the stimuli occur so rapidly (several hundred per second) that relaxation cannot occur between successive contractions. In most tetanic contractions the individual muscle fibers are stimulated in rotation, rather than simultaneously, so that although they contract and relax, the muscle as a whole remains partly contracted. From personal experience you know that any muscle of your body can contract to different degrees. This gradation of contraction is controlled through the nervous system: in a weak contraction only a small percentage of the muscle fibers are stimulated at one time; for a stronger contraction a larger percentage of muscle fibers contract simultaneously.

* This term should not be confused with tetany, the muscular spasms occurring in deficiencies of the parathyroid hormone, or with the disease tetanus (lockjaw), characterized by abnormal muscular contractions and caused by the tetanus bacillus.

Tonus. The term **tonus** or "tone" refers to the state of sustained partial contraction present in all normal skeletal muscles as long as the nerves to the muscle are intact.* Each muscle is normally stimulated by a continuous series of nerve impulses which cause a constant, slight contraction or tonus, and severing the nerve to a skeletal muscle eliminates tonus immediately. Tonus is, then, a mild state of tetanus, present at all times and involving only a small fraction of the fibers of a muscle at any one time. It is believed that the individual fibers contract in turn, working in relays, so that every contracting fiber has a chance to recover completely, while other fibers are contracting, before it is called upon to contract again.

2. The Chemistry of Muscle Contraction. A steam engine can convert only about 10 per cent of the heat energy of its fuel into useful work; the rest is wasted as heat. But muscles are able to use between 20 and 40 per cent of the chemical energy of the food molecules, such as glucose, in contraction. The remainder is converted into heat, but is not wholly wasted, since it is used to maintain the body temperature. In a cold place, if one refrains from contracting the muscles, the heat produced elsewhere in the body is insufficient to keep it warm. In these circumstances the muscles contract involuntarily (one "shivers"), and heat is produced thereby to restore and maintain normal body temperature.

Physiologists and biochemists have been attempting for many years to solve the problem of how protoplasm can exert a pull, and the problem is still far from solved. Chemical analysis reveals that muscle is about 80 per cent water, the rest being mostly protein, with small amounts of fat and glycogen, and two phosphorus-containing substances, **phosphocreatine** and **adenosine triphosphate.** The actual contractile part of a muscle fiber is believed to be a protein chain which shortens by folding. The theory is that the carbon and nitrogen atoms which are linked together to constitute the backbone of this chain, change their positions so that the chain alters from an extended form to a folded one. Two proteins are involved in this, **myosin,** and **actin,** neither of which is capable of contracting alone. But when they are mixed together in a test tube, and potassium and adenosine triphosphate are added, contraction does occur. This demonstration of contraction in a test tube, made by Dr. Albert Szent-Györgyi, is one of the most exciting discoveries yet made in biochemistry.

The first step in unraveling the mystery of contraction consists in making analyses to determine what substances are used up in the process. Glycogen, oxygen, phosphocreatine and adenosine triphosphate decrease in amount during contraction, and carbon dioxide, lactic acid (the acid of sour milk) and inorganic phosphate increase. The fact that oxygen is used up and carbon dioxide is formed suggests that muscular contraction is an oxidative process. But this oxidation is not essential, for a muscle can twitch a good many times even when completely deprived of oxygen—for example, when it is removed from the body and placed in an atmosphere of nitrogen. Such a muscle becomes fatigued, however, sooner than one contracting in an atmosphere of

* Cardiac and smooth muscles also exhibit tonus, even after their nerves are cut.

oxygen. Furthermore, although we breathe more rapidly during muscular exertion, the accelerated breathing continues for some time after the physical work has ceased. This suggests that oxidation is involved, not in muscular contraction, but in the process of recovery from contraction.

The disappearance of glycogen and the formation of lactic acid are related, for in the absence of oxygen, the amount of lactic acid formed is just equivalent to the glycogen that disappears.* Since the breakdown of glycogen to lactic acid requires no oxygen, and since it liberates energy rapidly, it was once thought that this reaction is directly responsible for muscle contraction. When oxygen is present, the muscle oxidizes about one fifth of the lactic acid to carbon dioxide and water, and the energy released by this oxidation is used to reconvert the other four fifths of the lactic acid to glycogen. This explains why lactic acid does not accumulate as long as muscle has sufficient oxygen, and why a muscle becomes fatigued more rapidly (uses up its glycogen and accumulates lactic acid) when it contracts in the absence of oxygen.

About 1930 it was found that when a muscle is poisoned with iodoacetate, which inhibits the chemical reactions by which glycogen breaks down to lactic acid, it can still contract, although it is capable of twitching only sixty to seventy times instead of the 200 or more times achieved by a muscle deprived of oxygen. But the fact that it can twitch at all when the breakdown of glycogen is prevented, shows that this is not the primary source of energy for contraction.

The other change that can be detected chemically during contraction is a breakdown of the organic phosphates—phosphocreatine and adenosine triphosphate—to inorganic phosphate and the corresponding organic compounds, accompanied by the release of energy. It is now believed that this reaction provides the immediate source of energy for contraction. After a contraction the organic phosphates reappear in the muscle, resynthesized from phosphate and the organic compounds. The energy required for this synthesis comes from the breakdown of glycogen to lactic acid.

The nature of the connection between phosphate and the organic compounds, creatine and adenylic acid, is different from that of most phosphate compounds, and has been called a "high energy" phosphate bond. This simply means that a great deal of energy (about 12,000 calories) is involved in holding the phosphate on to the organic compound, which is released when the bond is broken. The latest theory is that the major part, and perhaps all, of the energy needed by the body for all its processes must be converted into these "high energy" phosphate bonds to be available for use. This is the final step in the utilization of food. We mentioned in the discussion of metabolism that the oxidation of glucose to carbon dioxide and water was an extremely complicated process, involving the formation of phosphorus compounds. In the process of glucose oxidation, by way of these intermediate

* There are many intermediate steps between glycogen and lactic acid, but the overall chemical equation is as follows:

$$\underset{\text{glycogen}}{(C_6H_{10}O_5)_x} + X\ H_2O \longrightarrow \underset{\text{glucose}}{X\ C_6H_{12}O_6} \longrightarrow \underset{\text{lactic acid}}{2X\ C_3H_6O_3} + \text{energy}$$

phosphate compounds, the energy present in the molecule of sugar is transferred to these "high energy" phosphate compounds, and thus made available for the contraction of a muscle, the conduction of a nerve impulse, or the secretion of a substance by a gland, all of which require energy.

In summary, the chemistry of muscle contraction involves the following chemical reactions:

$$\text{Organic phosphates} \rightleftharpoons \text{Phosphate} + \text{Organic compounds} + \text{Energy (used in actual contraction)}$$

$$\text{Glycogen} \rightleftharpoons \text{Intermediates} \rightleftharpoons \text{Lactic acid} + \text{Energy (used in resynthesis of organic phosphates)}$$

$$\text{Part of lactic acid} + O_2 \longrightarrow CO_2 + H_2O + \text{Energy (used in resynthesis of rest of lactic acid to glycogen)}$$

3. The Oxygen Debt. The fact that the actual contraction, and part of the recovery from contraction, occur without oxygen is extremely important. Our muscles are often called upon to do great spurts of work, and although both the rate of breathing and the heart rate increase during exertion, oxygen cannot be supplied in sufficient quantities to permit these exertions. During violent exercise, such as running the 100 yard dash, glycogen breaks down to lactic acid faster than the lactic acid can be oxidized, so that the latter accumulates. In such circumstances the muscle is said to have incurred an **oxygen debt,** which is afterwards repaid by our rapidly breathing enough extra oxygen to oxidize part of the lactic acid, which furnishes energy for resynthesizing the rest to glycogen. During a long race a runner may reach an equilibrium in which he gets a "second wind," and, because of the increase in breathing and heart rate, takes in enough oxygen to oxidize the lactic acid formed at that moment, so that the oxygen debt is not increased.

4. Fatigue. A muscle that has contracted many times and exhausted its store of organic phosphates and glycogen, and accumulated lactic acid, is unable to contract any more and is said to be **fatigued.** Fatigue is primarily induced by this accumulation of lactic acid, although animals feel fatigue before the muscle reaches the exhausted condition.

The exact spot most susceptible to fatigue can be demonstrated experimentally if a muscle and its attached nerve are dissected out and the nerve stimulated repeatedly by electric shocks until the muscle no longer contracts (Fig. 121). If the muscle is then stimulated directly, by placing the electrodes on the muscle tissue, it will respond vigorously; and with the proper apparatus for detecting the passage of nerve currents, it can be shown that the nerve leading to the muscle is not fatigued, being still capable of conduction. The point of fatigue, then, is the *junction* between the nerve and the muscle, that point where the nerve impulses cause the muscle to contract.

5. The Nature of Contraction. At present there are two hypotheses of the nature of muscle contraction. One states that the energy for contraction is released from the organic phosphate to the muscle fiber at the moment of contraction, and that after this energy has been used in the physical shortening of the fiber, the fiber automatically relaxes.

The other states that contraction resembles the releasing of a stretched spring, the muscle before contraction being analogous to a spring that has been stretched and held by a kind of trigger mechanism. When this trigger is tripped by the nerve impulse, the spring contracts; energy is then required to restretch the spring for the next contraction. The latest evidence favors the second hypothesis, that energy must be supplied to make the muscle fiber *relax*, and that it contracts, releasing energy, when its "trigger" is pulled. When a muscle is stimulated repeatedly and becomes fatigued, it does not gradually lose its ability to contract; instead, its relaxations becomes slower and more labored, and when fully fatigued, it can no longer relax, but must remain contracted. This condition we call "cramps." After death, also, the muscles lose their power to relax and go into a state of contraction (the so-called *rigor mortis*), which lasts until the muscle fibers begin to disintegrate.

When a muscle contracts, it becomes shorter and fatter, but there is

Fig. 121. Fatigue. Contractions of a frog muscle (recorded by means of a kymograph) induced by rapidly repeated stimuli applied to the nerve of the muscle. When the muscle no longer responded to nerve stimulation, stimuli applied directly to the muscle (beginning at *M*) caused definite contractions, demonstrating that the fatigue was not primarily in the muscle itself. (Carlson and Johnson: The Machinery of the Body, published by University of Chicago Press.)

no change in its total volume. This has been shown experimentally by dissecting out a muscle, placing it in a glass vessel with a narrow neck, and filling the vessel with water. The muscle is then stimulated electrically, and as it contracts and relaxes, there is no change in the water level in the neck of the vessel.

6. Cardiac and Smooth Muscle. The muscles of the heart and internal organs, though resembling skeletal muscle in a general way, have certain distinctive characteristics. They are both much slower to contract than skeletal muscle: while skeletal muscle fibers contract and relax in 0.1 seconds, cardiac muscle requires from one to five seconds, and smooth muscle needs from three to 180 seconds. All the phases of contraction are prolonged.

Smooth muscle exhibits wide variations in tonus; it may remain almost relaxed or tightly contracted. And it also, apparently, can maintain the shortened condition of tonus without the expenditure of energy, perhaps owing to a reorganization of the protein chains making up the fibers.

Each beat of the heart represents a single twitch. Cardiac muscle has a long **refractory period**, the period following one stimulus when it is unable to respond to any other. Consequently, it is unable to contract tetanically, since one twitch cannot follow another quickly enough to maintain a contracted state.

7. The Muscles of Lower Animals. The muscles of all animals from the flatworm to man are similar in that they are all made of long cylindrical or spindle-shaped fibers which are contractile because of their protein chains. Even the coelenterates, which lack true muscle fibers, have cells which can contract. Differences do exist, however; for example, most of the invertebrates have only smooth muscle, whereas arthropods have only striated muscle. Electrical phenomena are associated with all types of muscle contraction, (cf. the electrocardiograph; p. 152), but in some animals, such as the electric eel, specialized muscle cells have evolved in which contraction is at a minimum and the production of electricity is at a maximum. The "electric organ" of the eel may produce a potential of 400 volts or more, sufficient to stun or kill the fish on which it preys, and to give quite a jolt to a man.

QUESTIONS

1. What are the three types of muscle fiber, and what are their distinguishing characteristics?
2. Describe a typical skeletal muscle.
3. What is tonus?
4. State the "All-or-None" Law. Does the muscle as a whole operate according to this principle? If not, what does control the degree of contractions?
5. What is tetanus?
6. What causes the phenomenon of shivering?
7. What is meant by the term "oxygen debt?"
8. Explain in detail how fatigue is caused.
9. What happens when a muscle contracts? When it relaxes?
10. What is responsible for the contractile quality of a muscle fiber?

SUPPLEMENTARY READINGS

Best, C. H., and Taylor, N. B.: *The Living Body*. New York, Henry Holt & Company, Inc., 1944.
A clear, understandable presentation of human physiology.

Carlson, A. J., and Johnson, V.: *The Machinery of the Body*. 3rd ed. Chicago, University of Chicago Press, 1948.
A well-written and illustrated discussion, on a fairly simple level, of human physiology.

Fulton, J. F.: *Howell's Physiology*. 16th ed. Philadelphia, W. B. Saunders Company, 1949.
One of the standard, detailed, advanced texts of physiology.

Gerard, R. W.: *The Body Functions*. New York, John Wiley & Sons, Inc., 1941.
An interesting account of circulation, digestion and excretion in man.

Szent-Györgyi, A.: *Chemistry of Muscular Contraction*. New York, Academic Press, Inc., 1947.
fascinating discussion, by one of the foremost research workers in the field, of some of the new ideas of how a muscle contracts.

CHAPTER 16

THE NERVOUS SYSTEM

TO KEEP the various parts of anything as complicated as the human body functioning properly requires a correspondingly complex coordinating device; the nervous system, which integrates the activities of all the parts of the body, is undoubtedly the most complex of all the body systems. The muscles and glands of an animal are collectively called **effectors;** the eyes, ears and other sense organs are known as the **receptors.** The nervous system, composed of brain, spinal cord and nerve trunks, connects receptors with effectors and conducts impulses or "messages" from one to the other. It is able to do all this in such a way that the proper effector responds when a given receptor is stimulated. The two chief functions of the nervous system are, then, **conduction** and **integration.**

1. Neurons. Although their interrelations are exceedingly complex, the cells which constitute the nervous system, called **neurons,** are all fundamentally similar, consisting of one or more **axons,** one or more **dendrites** (see p. 43), and, in between, a **cell body,** containing the nucleus. Neurons differ widely in the shape of the cell body, and in the length, number and amount of branching of the axons and dendrites. They are subdivided into **sensory, motor** and **connector** neurons on the basis of their connections. Thus, sensory neurons have their dendrites connected to receptors, and their axons connected to other neurons; motor neurons have their dendrites connected to other neurons, and their axons to some effector; connector neurons have both dendrites and axons connected to other neurons. The simplest pathway that a nerve impulse can follow consists of one sensory, one connector and one motor neuron.

The **nerve trunks** or **nerves** of the body consist of large numbers of axons and dendrites bound together in a common connective tissue sheath. The cell bodies of the neurons are not scattered at random along these nerve trunks, but occur in aggregations, called **ganglia** if they occur outside the brain and spinal cord, and **nerve centers** if they occur within the brain or spinal cord.

In addition to and surrounding the cell membrane of the axon and dendrite, may be one or two nerve sheaths, an outer **neurilemma** and an inner **myelin** sheath (Fig. 122). The neurilemma sheath is cellular. The myelin sheath is composed of noncellular, fatty substances which give a white appearance to nerves which have it. Nerve fibers in the spinal cord and brain have *only* a myelin sheath. Those going to the viscera have a neurilemma sheath and a thin myelin sheath, so that they are gray rather than white. Nerves to the skin and skeletal muscles have both sheaths.

The function of these sheaths is not clear. The position of the myelin sheath suggests that it may act as insulation, preventing the nerve impulse from passing from one fiber to another and thus causing the wrong effector to be stimulated, but there is no positive evidence for this suggestion. Or one might suppose that the myelin sheath acts as a reserve supply of nourishment for the fiber, but the available evidence indicates that the fiber receives its nourishment solely from the cell body. Another theory is that the myelin sheath functions to increase the speed of conduction of the nerve impulse. In man and other mammals a nerve impulse is conducted about 300 feet per second in a myelinated nerve, and 25 to 50 feet per second in the nerves going to the internal organs, which have only a thin myelin sheath. But there is no proof that the greater speed of conduction of the former is due to the myelin sheath and not to some other property of the nerve.

The neurilemma sheath seems to play some role in the regeneration of a cut nerve fiber (axon or dendrite). When fibers are severed, the parts

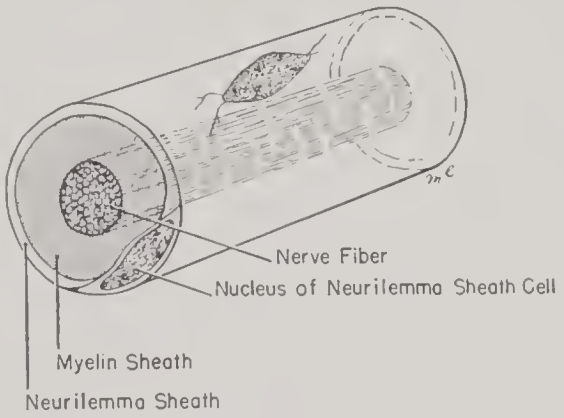


Fig. 122. A typical nerve fiber and its surrounding sheaths.

on the side of the cut away from the cell bodies degenerate and disappear in a few weeks, leaving the hollow tubes of the neurilemma sheaths. If the cut ends of the whole nerve trunk are then clamped or sewed together, the nerve fibers may grow from the cut ends out through the tubes formed by the neurilemma sheaths which surrounded the degenerated fibers, to the structures innervated by the original fibers. In this way the sensations and muscular control lost when the nerve was cut may be regained. The length of time required for regeneration depends on how far the nerve has to grow; as much as two years may be necessary. When a cut occurs in the brain or spinal cord, where the fibers have no neurilemma sheath, regeneration does not occur. Whether the neurilemma simply directs the course of the regenerating fiber or aids in its nourishment, or has some other function, is not known.

2. The Nerve Impulse. The study of the nature of the nerve impulse has been fraught with special difficulties because nothing visible occurs when an impulse passes along a nerve. Only recently, with the development of techniques for measuring infinitesimal chemical changes, has it been possible to show that the nerve fiber must expend more energy, consume more oxygen and give off more carbon dioxide and heat while transmitting an impulse than it does in a resting state. This indicates that oxidative processes are involved in the conduction of an impulse, or in the recovery of the nerve after conduction, or both.

With the discovery, about a century ago, that the nerve impulse is accompanied by certain electrical changes, arose the belief that the impulse itself is an electric current. At that time the speed of electricity was known to be fast, and it was predicted that the speed of the nerve impulse, being just as fast, could not be measured. Ten years later, Helmholz measured the speed of impulse conduction in nerves by stimulating the nerve to a muscle at different distances from the muscle, and measuring the elapsed time between stimulus and contraction. In this way he demonstrated that the nerve impulse travels much more slowly than electricity—at about 100 feet per second in frog nerves. This, of course, was evidence that the nerve impulse is not an electric current similar to that in a copper wire. Furthermore, dead or crushed nerves still conduct electricity, but not nerve impulses, and whether a nerve is stimulated electrically or by touch, heat or chemicals, the resulting impulse travels at the same rate of speed. A nerve impulse, then, is not an electric current, but an **electrochemical disturbance** in the nerve fiber. A stimulus instigating this disturbance in one section of a nerve fiber causes a similar disturbance in the adjacent section, and so on until the impulse reaches the end of the fiber. The transmission of an impulse is thus analogous to the burning of a fuse: the heat given off by the burning of one section causes the next section to catch fire, and so on. Of course, in the nerve, it is not the heat given off by one section which stimulates the next, but the electrical changes which occur.

The transmission of the nerve impulse shows further similarities to the burning of a fuse. The rate at which a fuse burns is independent of the amount of heat applied to light it, provided enough heat is applied to light it at all. Furthermore, the method of setting it off is unimportant. The same thing is true of a nerve. It will not respond unless a stimulus of a certain minimum intensity is applied, but increasing the strength of the stimulus beyond this minimum does not cause the impulse to travel any faster. This is due to the fact that energy for conducting the impulse is derived from the nerve itself and not from the stimulus. The phenomenon is expressed in the **All-or-None Law:** the nerve impulse is independent of the nature or strength of the stimulus setting it off, if the stimulus is strong enough to set it off at all. But although the rate of conduction is independent of the strength of the stimulus, it does depend on the state of the nerve fiber, and drugs can retard or prevent the transmission of an impulse.

The analogy between a fuse and a nerve breaks down, because a burned fuse is gone forever, while a nerve fiber is capable of recovering and transmitting other impulses. It does not do this immediately, however; a definite period of time elapses after the passage of one impulse before the fiber can transmit another. This interval, known as the **refractory period,** lasts from 0.001 to 0.005 second. During this time, chemical and physical changes occur which restore the fiber to its original condition.

So far as we know, the impulses transmitted by all types of neurons—motor, sensory and connector—are essentially alike. The fact that one impulse results in a sensation of sight, another in a sensation of sound, another in muscle contraction, and another in glandular secretion, is

due entirely to the nature of the structures to which the impulses travel, and not to any peculiarity of the impulses themselves.

Although a nerve fiber can be stimulated anywhere along its length, stimulation normally occurs at one end only, from which the impulse passes along the fiber to the other end.* The junction between consecutive neurons is called a **synapse.** A nerve impulse is transmitted from the tip of the axon of one neuron to the dendrite of the next across the synaptic junction by means of a chemical secretion at the tip of the axon. This initiates a nerve impulse in the dendrite of the next neuron. Transmission across the synapse is considerably slower than transmission along the nerve. Impulses normally pass in one direction only: those in sensory neurons pass from the sense organs to the spinal cord and brain; those in motor neurons, from the brain and spinal cord to the muscles and glands. The synapse controls this, because only the tip of the axon is capable of secreting the chemical which stimulates the next neuron. Any individual nerve fiber can conduct an impulse in either direction; if it is stimulated electrically in the middle, two impulses will be set up, one going in one direction and one in the other (these can be detected by appropriate electrical devices), but only the one going *toward* the *axon* can stimulate the next neuron in line. The one going toward the dendrite will stop when it arrives at the tip.

The chemical and electrical processes involved in the transmission of a nerve impulse are similar in many ways to those involved in muscle contraction. But a transmitting nerve expends little energy compared to a contracting muscle; the heat produced by 1 gm. of nerve, stimulated for one minute, is equivalent to the energy liberated by the oxidation of 0.000001 gm. of glycogen. This means that if a nerve contained only 1 per cent glycogen to serve as fuel, it could be stimulated continuously for a week without exhausting the supply. Nerve fibers are practically incapable of being fatigued as long as an adequate supply of oxygen is available. Whatever mental fatigue may be, it is not a real fatigue of the nerve fibers.

The generally accepted theory of the nature of the nerve impulse is the **membrane theory.** According to this, the membrane surrounding each nerve fiber is semipermeable, allowing certain ions, but not all, to penetrate it. The metabolic activities of the nerve maintain this membrane in a polarized state; that is, there is an extra number of positive ions (positively charged chemical particles) on its outer surface, and an equal excess of negative ions on its inner surface, so that the resting nerve resembles a charged condenser (Fig. 123). The positive and negative ions are kept from mixing, and neutralizing each other, by the membrane, which is impermeable to them. The potential across the membrane due to the excess of positive ions outside and negative ions inside is from 0.03 to 0.06 volts.

When a nerve is stimulated at one point, the stimulation depolarizes

* The only nerve that is occasionally stimulated at a point along its length, as well as at the end, is the "crazy bone" nerve, or ulnar nerve, which lies close to the surface of the skin at the elbow. This nerve is made up of fibers for pain, touch, cold, pressure, and so on, which is why one receives the tingling, "mixed" sensation when it is bumped. The other nerves are imbedded so deep in the tissue that they are not vulnerable to such stimulation; but if they were so stimulated, artificially, the same peculiar sensation would result.

the membrane and increases its permeability, so that the ions from the adjacent, not-yet-activated region pass through the depolarized region and neutralize each other (Fig. 123). This depolarizes the adjacent region and makes it permeable to the migration of ions from the next region, and so on. In this way the nerve impulse moves along the surface of the nerve fiber as a wave of depolarization of the membrane. It seems

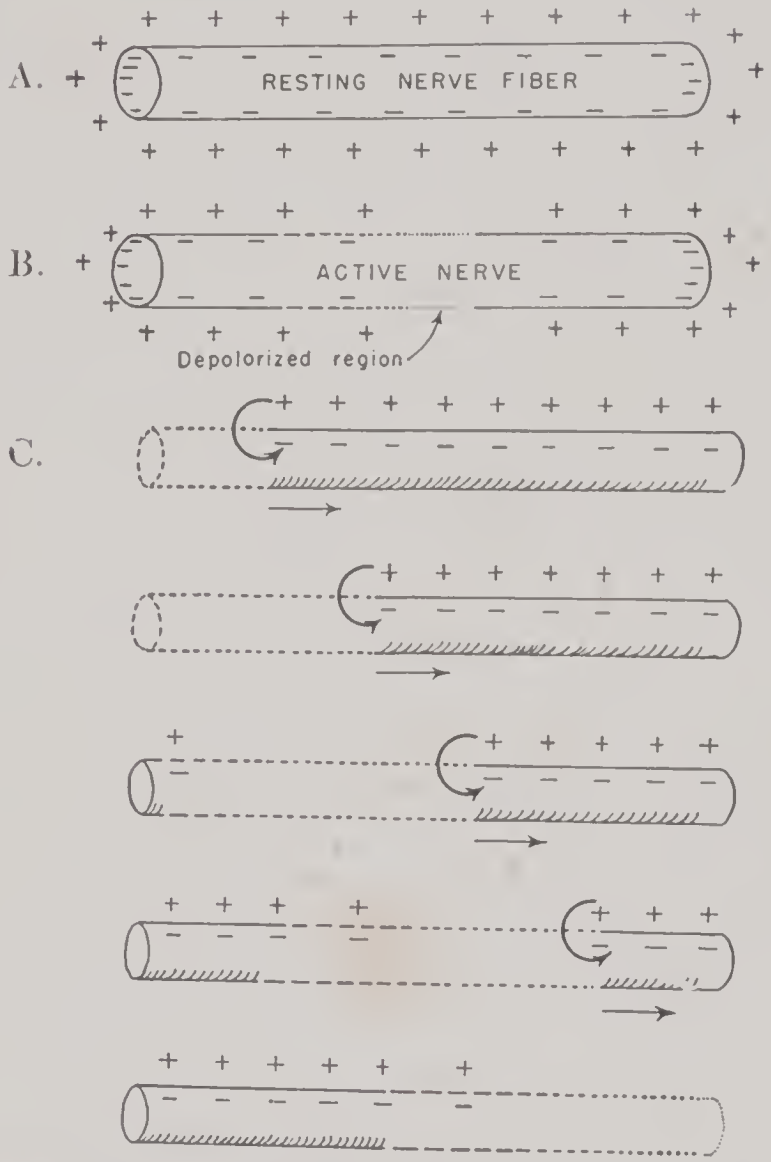


Fig. 123. Diagram illustrating the membrane theory of nerve transmission. *A*, Resting nerve, showing the polarization of the membrane with positive charges on the outside and negative ones inside. *B*, Nerve conducting an impulse, showing, from left to right, the partially repolarized region behind the impulse, the depolarized region where the impulse is, and the polarized region ahead of the impulse. *C*, Stages in the passage of the impulse along the nerve. (Hunter and Hunter: College Zoology.)

probable that some chemical reactions must occur in the depolarized membrane to make it permeable, and other reactions must occur during the refractory period to recharge the membrane and prepare it to be depolarized by the next impulse. Although there are many other details, the transmission of the nerve impulse rests on this rather simple electrochemical mechanism. All the complex phenomena of reflexes, learning and creative thinking depend on these extremely feeble currents and small chemical changes.

This theory, which is supported by all the experimental evidence, affords an explanation of the refractory period as the time necessary to

repolarize the membrane. And it accounts also for the all-or-none phenomenon, since no matter what the strength of the stimulus, the depolarization can go only as far as zero.

3. Transmission at the Synapse. The process whereby a nerve impulse is transmitted across a synapse from one neuron to the next is not perfectly understood. It was once believed that an impulse reaching the end of one neuron simply excites the next one as though it were a continuation of the first, and this may actually happen at certain synapses. But at others a completely different mechanism operates, one which depends on the secretion of a chemical substance, called a neurohumor, by the tip of the axon. This chemical then diffuses to the dendrite of the next neuron or to the muscle or gland innervated, and stimulates it.

The existence of these chemicals was discovered in experiments on the heart, an organ supplied with two sets of nerves, one which speeds it up, another which slows it down. When a frog's heart is isolated from the body, and the vagus (inhibitory) nerve to it is stimulated, it stops beating. If the heart is then washed out with salt solution, and the fluid is placed in a second heart, the latter also stops! Therefore, the vagus nerve must release some chemical which inhibits the heart beat. Further research has shown this substance to be a relatively simple chemical called **acetylcholine;** pure, synthetic acetylcholine has the same effect. Here the chemical transmission is from nerve to muscle, but the same mechanism is involved in at least some types of synapses between two neurons. By similar experiments it has been shown that the nerves speeding up the heart also release a chemical substance, called **sympathin,** which is similar to or identical with the hormone epinephrine. You many wonder why, if the tip of the axon secretes a substance such as acetylcholine, that substance does not stimulate the next dendrite or the muscle continuously. The answer is that blood and most tissues contain a potent enzyme, called **cholinesterase,** which specifically destroys acetylcholine, thereby preventing its continued effect. A different enzyme oxidizes sympathin.

It is not yet definitely known whether transmission across the synapses in the brain and spinal cord is by means of acetylcholine, sympathin or some other chemical, or by an electrical mechanism.

The synaptic junction is a point of resistance to the flow of impulses in the nervous system, and not every impulse reaching the synapse is transmitted to the next neuron. The resistance varies in different synapses, so that they are important in determining the route of impulses through the nervous system and the response of the organism to a specific stimulus.

Functionally, the entire nervous system is a unit, and an impulse arising in any receptor can be transmitted to every effector in the body. Consider, for example, the effects of burning a finger: the muscles of the arm contract to pull the finger away from the heat, a sensation of pain is produced in the brain, a cry may be emitted, the heart beat, digestion and breathing may be interrupted—in fact, it is conceivable that every muscle and gland in the body may be affected temporarily. Since our sense organs are being stimulated constantly, you may wonder why all the muscles and glands are not constantly contracting and

secreting. That they are not is due to the selective resistance at the synaptic junction.*

The amount of synaptic resistance can be modified by nerve impulses, so that one impulse cancels out the effect of another. This is known as **inhibition.** The opposite condition, whereby one impulse strengthens another, is called **reinforcement.** These two processes are of prime importance in effecting integration of body activities. We have seen that all the muscles of the body are in a state of constant, slight contraction, known as tonus, due to a constant volley of nerve impulses reaching them. But when one muscle, such as the triceps, is to contract, its antagonist, the biceps, must relax. This is achieved by the simultaneous operation of impulses which inhibit the volley of impulses to the biceps, and of impulses which reinforce the volley to the triceps. Inhibition and reinforcement can occur only at the synapse, since once an impulse starts along a neuron, it can be neither stopped nor accelerated. Whether or not a given impulse crosses a synapse depends on whether it is inhibited or reinforced by other impulses.

I. THE PARTS OF THE NERVOUS SYSTEM

The ten billion or so neurons which make up the nervous system are divided into two main parts: those belonging to the **central nervous system,** which make up the brain and spinal cord, and those belonging to the **peripheral nervous system,** which make up the cranial and spinal nerves.

4. The Central Nervous System: *The Spinal Cord.* The tubular spinal cord, which is surrounded and protected by the neural arches of the vertebrae, has two important functions: to transmit impulses to and from the brain, and to act as a reflex center. In cross section it is seen to consist of two regions, an inner, butterfly-shaped mass of gray matter, made up of nerve cell bodies, and an outer mass of white matter made up of bundles of axons and dendrites (Fig. 124). The whiteness of these bundles is due to the myelin sheaths of the axons and dendrites; the ends of the axons and dendrites, present in the central gray matter, have no myelin sheath. The "wings" of the gray matter are divided into two dorsal horns and two ventral horns. The latter contain the cell bodies of motor neurons, whose axons pass out through the spinal nerves to the muscles; all the other neurons in the spinal cord are connector neurons.

The axons and dendrites of the white matter are segregated into bundles with similar functions: the **ascending tracts,** which carry impulses to the brain, and the **descending tracts,** which carry impulses from the brain to the effectors. Neurologists have patiently collected data on persons with injured spinal cords, and by carefully noting the symptoms, and correlating these with the particular tracts found to be destroyed when the patient's nervous system was examined after death, they have been able to map out the location and functions of the various tracts (Fig. 124). For example, the dorsal columns of the white matter transmit impulses originating in the sense organs of muscles, tendons

* What would occur in the absence of this synaptic mechanism can be seen in a person suffering from strychnine poisoning. Strychnine has the effect of decreasing the synaptic resistance, so that the slightest stimulus sets off the convulsive contraction of all the muscles of the body.

and joints, by means of which we are aware of the position of the parts of the body. Often in advanced syphilis these columns are destroyed, so that the patient cannot tell where his arms and legs are unless he looks at them, and he must watch his feet in order to walk.

One curious fact, still not satisfactorily explained, emerged from these studies of the location and function of the fiber tracts. All the fibers in the spinal cord cross over from one side of the body to the other somewhere along their path from sense organ to brain, or from brain to muscle. Thus the right side of the brain controls the left side of the

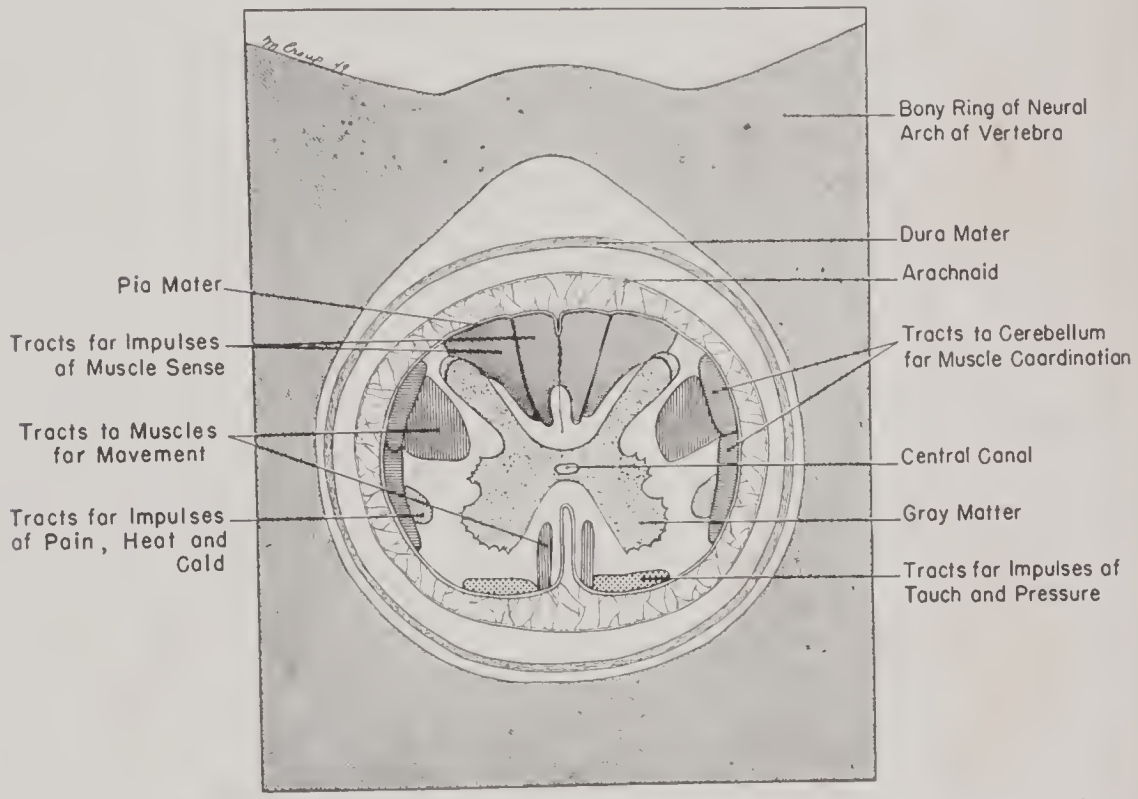

Bony Ring of Neural Arch of Vertebra
Dura Mater
Arachnoid
Pia Mater
Tracts for Impulses of Muscle Sense
Tracts to Cerebellum for Muscle Coordination
Tracts to Muscles for Movement
Central Canal
Tracts for Impulses of Pain, Heat and Cold
Gray Matter
Tracts for Impulses of Touch and Pressure

Fig. 124. Cross section of the spinal cord surrounded by the bony vertebra, showing the meninges (*dura mater, pia mater* and *arachnoid*), the gray matter, and some of the important nerve tracts of the white matter.

body and receives impressions from the sense organs of the left side. Some fibers cross in the spinal cord itself; others cross in the brain.

In the center of the gray matter is a small canal, running the entire length of the spinal cord, filled with **cerebrospinal fluid**, which is similar to plasma. The spinal cord and brain are wrapped in three sheets of connective tissue, known as **meninges.*** One of these sheets (dura mater) is fastened against the bony neural arches of the vertebras; another (pia mater) is located on the surface of the spinal cord, and the third (arachnoid) lies between. The spaces between the meninges are filled with more cerebrospinal fluid, so that the spinal cord (and the brain) floats in this liquid and is protected from bouncing against the bone of the vertebras (or skull) with every movement.

The Brain. There is a general correlation between the size of the brain and what we call intelligence. Modern man has a brain volume of about 1500 cc., while the higher apes have a brain size of only 600 cc. Our immediate evolutionary ancestors had intermediate-sized brains: Java man, 940 cc.; Peking man, 1000 cc.; Piltdown man, 1350 cc.; and Ne-

* Meningitis is a disease in which these wrappings become infected and inflamed.

anderthal man, 1550 cc. The important factor is not absolute, but relative, size, however, since a whale with a 3000 cc. brain is not so intelligent as a rat with a 20 cc. brain. And even the ratio of brain weight to total body weight is not completely valid, for some vertebrates, notably certain monkeys, have a higher such ratio than man. Intelligence can best be correlated with the ratio of brain weight to spinal cord weight, which indicates the extent of the control of the higher centers over the lower. In frogs and fishes this ratio is less than one; the brain weighs less than the spinal cord. In lower mammals it is between two and four; in apes, fifteen; and in man the brain weighs fifty-five times as much as the spinal cord.

The brain is the enlarged, anterior end of the spinal cord. In man the enlargement is so great that much of the resemblance to the spinal cord is obscured, but in the lower animals the relationship of brain to spinal cord is clear. The detailed anatomy of the brain is exceedingly complex, and we shall consider only the six main regions: medulla, pons, cerebellum, midbrain, thalamus and cerebrum (Fig. 125).

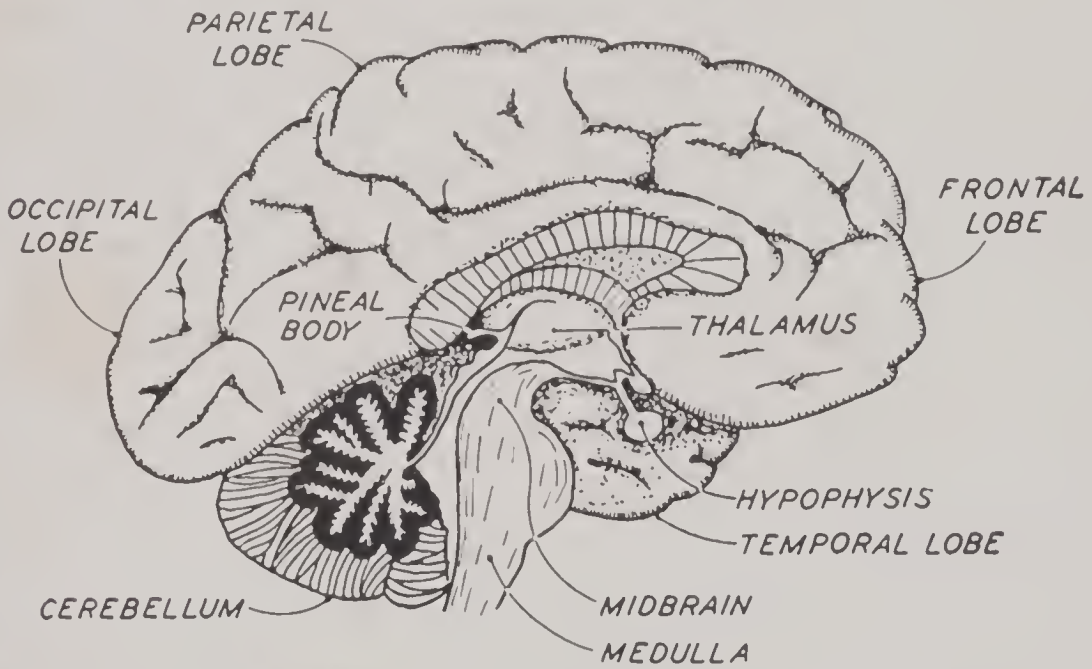


Fig. 125. The brain as seen in a median sagittal section. (Carlson and Johnson: The Machinery of the Body, 3rd Ed., published by University of Chicago Press.)

The most posterior part of the brain, lying next to the spinal cord, is the **medulla**. Here the central canal of the spinal cord enlarges to form a large cavity called the fourth ventricle (three other ventricles lie farther up in the brain). The roof of the fourth ventricle is thin and contains a cluster of blood vessels which secrete part of the cerebrospinal fluid; the rest of this fluid is secreted by similar clusters of blood vessels in the other ventricles. In the roof of the fourth ventricle are three tiny pores through which the cerebrospinal fluid escapes into the meningeal spaces. The walls of the medulla are thick and made up largely of nerve tracts connecting with the higher parts of the brain. The medulla also contains a number of clusters of nerve cell bodies, the **nerve centers**, which are reflex centers controlling many of the fundamental physiological processes of the body—respiration, heart rate, the dilatation and constriction of blood vessels, swallowing and vomiting.

Above the medulla is the **cerebellum,** consisting of a central part, and two hemispheres extending laterally, which resemble pine cones in shape. Its gray surface is made up of nerve cell bodies, and beneath is a mass of white tissue composed of fiber tracts connecting with the medulla and with the higher parts of the brain. The size of the cerebellum in different animals is roughly correlated with the amount of their muscular activity. Since it regulates and coordinates muscle contraction, it is proportionately large in extremely active animals, such as birds. Removal or injury of the cerebellum is not accompanied by paralysis, but by impairment of muscle coordination. When the cerebellum of a bird is removed surgically, it is unable to fly and the wings thrash about jerkily. When the human cerebellum is injured by a blow or disease, all muscular movements are uncoordinated, and any activity requiring delicate coordination, such as threading a needle, is impossible.

Running crosswise on the ventral side of the brain just below the cerebellum is a thick bundle of fibers, known as the **pons** or bridge, which carries impulses from one hemisphere of the cerebellum to the other, thus coordinating muscle movements on the two sides of the body.

In front of the cerebellum and pons lies the **midbrain,** which has thick walls and a small central canal connecting the fourth ventricle of the medulla with the third ventricle in the thalamus. The thick walls of the midbrain contain certain reflex centers and the main fiber tracts leading to the thalamus and cerebrum. On the upper side of the midbrain are four low, rounded protuberances called **optic lobes,** in which are centers for certain visual and auditory reflexes. The reflex constriction of the pupil when light shines on the eye is controlled by a center in the optic lobes, as is the pricking up of a dog's ears in response to a sound. The midbrain also contains a cluster of nerve cells regulating muscle tonus and posture.

In front of the midbrain the central canal again widens and becomes the third ventricle, the roof of which contains another cluster of blood vessels secreting cerebrospinal fluid. The thick walls of the third ventricle are called the **thalamus.** This is a relay center for sensory impulses; fibers from the spinal cord and lower parts of the brain synapse here with other neurons going to the various sensory areas of the cerebrum. In the floor of the third ventricle are centers regulating body temperature, water balance, carbohydrate and fat metabolism, blood pressure and sleep. Curiously, the front part of the thalamus prevents a rise in body temperature and the rear part prevents a fall. The thalamus also appears to regulate and coordinate the external manifestations of emotions; thus, by stimulating the thalamus, a sham rage can be produced in a cat—the hair stands on end, the claws protrude, the back becomes humped, and other signs of anger are evinced. But as soon as the stimulation stops, the appearance of rage ceases.

The parts of the brain considered so far have to do with unlearned, automatic behavior which is determined by the fundamental structure of these parts, a structure which is essentially the same from fish to man. The **cerebrum,** the most anterior and the largest single part of the human brain, has a basically different function, that of controlling learned behavior. The complex psychological phenomena of consciousness, intelligence, memory, insight and the interpretation of sensations

have their physiological basis in the activities of the neurons of the cerebrum. The importance of the cerebrum to different animals can be investigated by removing it surgically. A cerebrumless frog behaves almost exactly as a normal one, and a pigeon whose cerebral cortex has been removed can fly and balance on a perch, but tends to remain quiet for hours. When stimulated, it moves about, though in a random, purposeless way, and since it fails to eat when given food, will starve unless fed artificially. A dog whose cerebral cortex has been removed can walk and will swallow food if it is placed in the mouth, but shows no signs of fear or excitement. Human infants occasionally are born whose cerebral cortex fails to develop, and although they can carry out the vegetative functions of breathing and swallowing, they are incapable of learning and make no voluntary movements. Such creatures usually die soon after birth.

The cerebrum contains slightly more than half of the ten billion neurons of the human nervous system. These are arranged in two **cerebral hemispheres,** which develop as outgrowths of the anterior end of the brain. In man and other mammals they grow back over the rest of the brain and hide it from view. Each hemisphere contains a cavity, the first and second ventricles, each of which is connected to the third ventricle of the thalamus by a canal. These ventricles, like the others, contain clusters of blood vessels which secrete the cerebrospinal fluid. The cerebrum is made of both gray and white matter; the latter, composed of tracts of nerve fibers, is on the inside of the cerebrum, while the gray matter, made of nerve cell bodies, lies on the surface or **cortex** of the cerebrum. Deep in the substance of the cerebral hemispheres lie other masses of gray matter, nerve centers which act as relay stations to and from the cortex. The lower vertebrates, with little gray matter, have smooth cerebral cortices, but in man and other mammals the surface of the cerebral hemispheres is convoluted. Ridges separated by furrows increase the amount of space available for the cortical gray matter. The pattern of these convolutions is quite constant even in men of widely different degrees of intelligence, and the geography of the cerebral cortex has been carefully studied (Fig. 126). The idea that certain parts of the brain have special functions is an old one, the "science" of phrenology having been based on the premise that functions were localized in the brain, so that if a person were specially gifted, a particular area would be enlarged and cause a bump on the head. It was believed that an analysis of such bumps would indicate what a man was best fitted for. How a tissue as soft as the brain could cause a bump in the hard skull was never considered.

Experimental evidence has established that there is a considerable amount of localization of function in the cortex. By surgical removal of particular regions of the cortex from experimental animals it has been possible to localize many functions exactly; and by observing the paralysis or loss of sensation in a man with a brain injury or tumor, and then examining the brain after death to see where the injury was located, it has been possible to map the human brain. During operations on the brain, surgeons have electrically stimulated small regions and observed which muscles contracted, and, since brain surgery can be carried on under local anesthesia, the patient could be asked what sensations he felt when the

particular regions were stimulated. Curiously, the brain itself has no nerve endings of pain, so that stimulation of the cortex is not painful. The most recent method of studying brain activity is that of measuring and recording the electrical potentials or "brain waves" given off by various parts of the brain when active (see p. 277).

By combining the data obtained in several ways, investigators have been able to locate many functions of the brain (Fig. 126). The back part contains the visual center; removal of it causes blindness, and stimulation of it, even by a blow on the back of the head, causes the sensation of light. Removal of the region from one side of the brain only, causes blindness in half of each eye, for the nerves from each eye

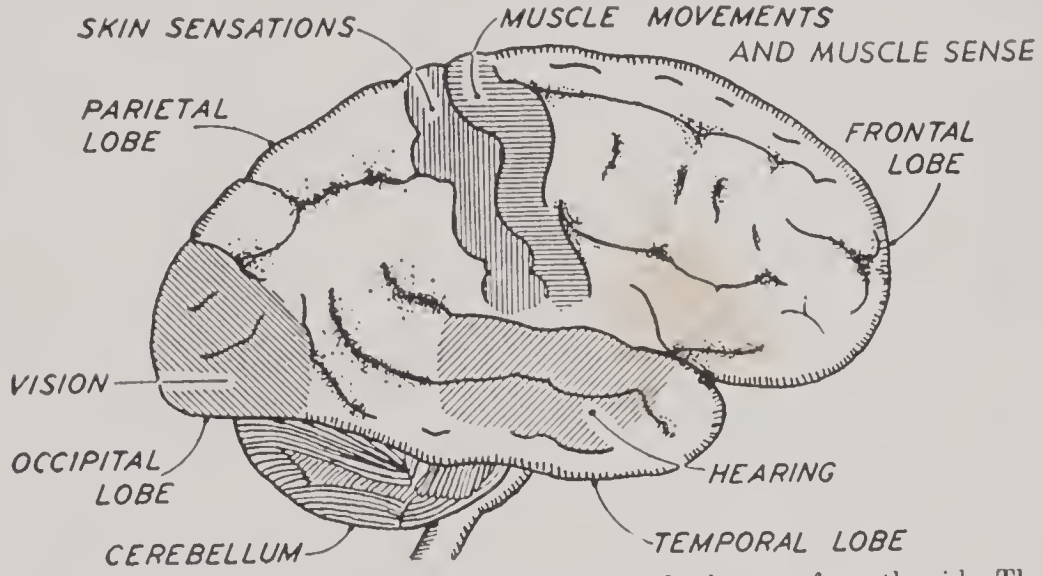


Fig. 126. The right cerebral hemisphere of the human brain, seen from the side. The areas concerned with special functions are indicated; the large, unshaded regions are the association areas. (Carlson and Johnson: The Machinery of the Body, 3rd Ed., published by University of Chicago Press.)

split, and half go to each side of the brain. The center for hearing is located on the side of the brain, above the ear. Stimulation of it by a blow causes a sensation of noise; although removal of both auditory areas causes deafness, removal of one does not cause deafness in one ear, but a decrease in the auditory acuity of both ears.

Running down the side of the cerebral cortex is an easily recognizable, deep furrow, called the fissure of Rolando, which separates the motor area, controlling the skeletal muscles, from the area just behind the furrow which is responsible for the sensations of heat, cold, touch and pressure upon stimulation of sense organs in the skin. In both there is a further specialization along the furrow from the top of the brain to the side—neurons at the top of the cortex control the muscles of the feet; the next in line control those of the shank, thigh, abdomen, and so on; and the neurons farthest around to the side control the muscles of the face. There is a similar relationship between the parts of the sensory area and the region of the skin from which it receives impulses. Thus, in the connections between the body and the brain, there is not only a twisting of the fibers so that one side of the brain controls the opposite side of the body, but a further "reversal" which makes the uppermost part of the cortex control the lower extremities of the body.

When all the areas of known function are plotted, they cover almost all of the rat's cortex, a large part of the dog's, a moderate amount of the monkey's, but only a small part of the total surface of man's cortex. The rest, known as **association areas,** is made up of neurons that are not directly connected to sense organs or muscles, but which supply interconnections between the other areas. These regions are responsible for the higher intellectual faculties of memory, reasoning, learning, imagination, and for personality. In some way, the association regions integrate all the diverse impulses constantly reaching the brain into a meaningful unit, so that the proper response is made. They interpret and manipulate the symbols and words by means of which our thought processes are carried on. When disease or accident destroys the functioning of one or more association areas, the condition known as **aphasia** results, in which the ability to recognize certain kinds of symbols is lost. In one type of aphasia the patient is unable to understand written words, although he comprehends spoken words perfectly. In another type of aphasia the names of objects are forgotten, although their functions are remembered and understood.

5. Brain Waves. Metabolism is invariably accompanied by electrical changes, and the electrical activity of the brain can be recorded by a device known as the electroencephalograph. To obtain recordings, electrodes are fastened to different parts of the scalp by adhesive tape, and the activity of the underlying parts of the cortex is measured. The electroencephalograph has shown that the brain is continuously active, even when no thinking is going on, and that the most regular manifestations, called alpha waves, come from the visual areas at the back of the brain when the subject is resting quietly with his eyes shut. These waves occur rhythmically at the rate of nine or ten per second and have a potential of about 45 microvolts (Fig. 127). When the eyes are opened, the waves disappear and are replaced by more rapid, irregular waves. That the latter are produced by objects seen can be demonstrated by presenting the eyes with some regular stimulus, such as a light blinking at regular intervals, and observing that brain waves of a similar rhythm appear. Sleep is the only normal condition in which the brain waves are drastically altered. During sleep the waves become slower and larger (have a greater potential) as the subject falls into deeper and deeper unconsciousness. The dreams of a sleeping subject are mirrored in flurries of irregular waves.

Certain brain diseases alter the character of the waves; epileptics, for example, exhibit a peculiar and readily recognizable wave pattern, and even people who have never had an epileptic attack, but might in certain conditions, show similar abnormalities. The location of brain tumors can be detected by noting the part of the brain showing abnormal waves.

6. Sleep. The neural mechanisms involved in sleep are unknown, and investigators are still trying to discover why sleep is necessary and why it has a recuperative effect. But whatever the reasons, it is absolutely certain that sleep is essential to life; any animal deprived of it for several days will die. Fatigue is popularly considered the cause of sleep, but there is no experimental evidence to verify this belief. The latest

findings indicate that a more important sleep-inducing factor is the absence of stimuli, and indeed everyday experience teaches that it is easy to go to sleep, even when one is not particularly tired, if there is nothing interesting to occupy the mind. But although we tend to be wakeful in the presence of attention-holding stimuli, there is a limit beyond which sleep is inevitable. Mental fatigue is not comparable to physical fatigue, however, and the factors determining the threshold of sleep are still not understood. For all the higher animals, life is characterized by a basic rhythm of sleep alternating with wakefulness, a pattern regulated in some way by the hypothalamus. The human habit of sleeping for eight hours of the twenty-four is definitely learned, since

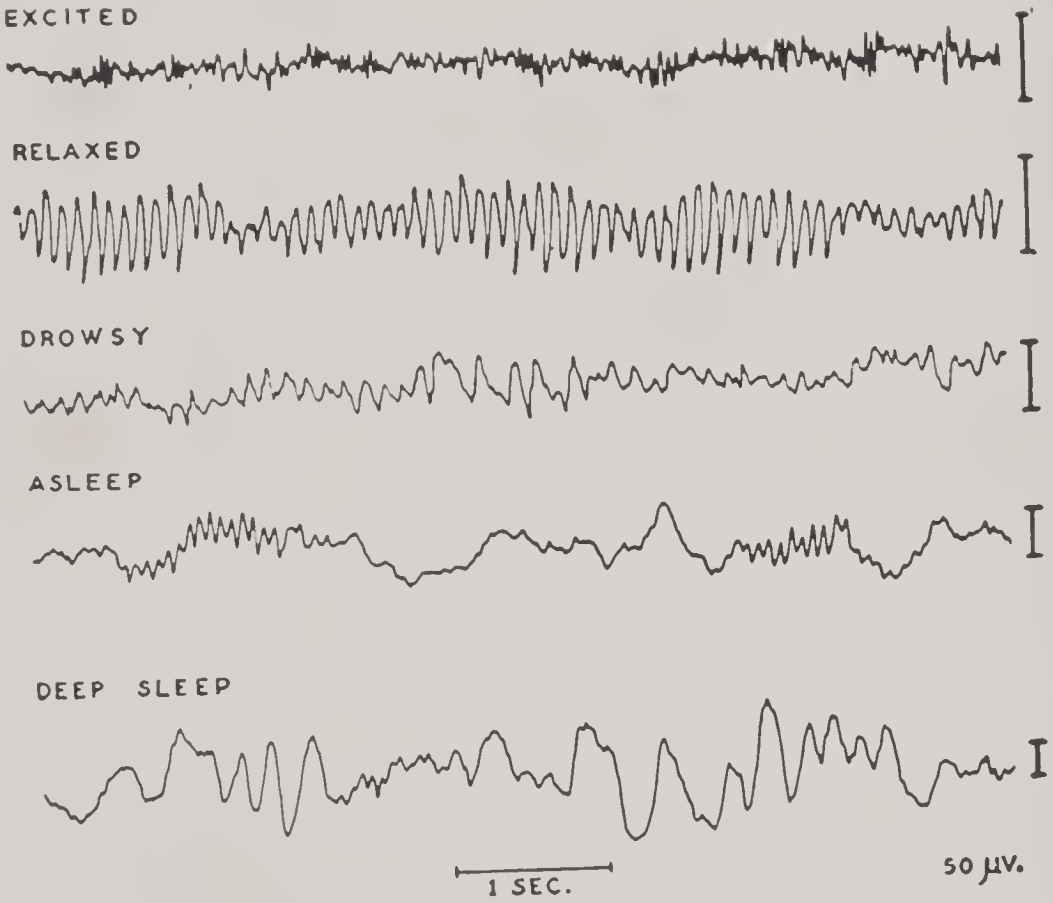


Fig. 127. Electroencephalograms made while the subject was excited, relaxed, and in various stages of sleep. Recordings made during excitement show brain waves which are rapid and of small amplitude, whereas in sleep the waves are much slower and of greater amplitude. The regular waves characteristic of the relaxed state are called alpha waves. (From Jasper; in Epilepsy and Cerebral Localization, by Penfield and Erickson.)

the basic, natural rhythm is one in which sleep and wakefulness alternate every three or four hours, as exemplified by the behavior of infants.

People differ as to the time of day when their ability to perform acts of skill is at a maximum. For some it seems to be a period soon after waking in the morning; for others, a period early in the afternoon. It is believed that mental acuteness and manual dexterity reach a peak when the temperature of the body is highest.

7. Insanity and Neuroses. Certain types of brain derangements have an easily understood basis in damage to the brain tissue produced by disease or a wound. If the pores in the roof of the fourth ventricle become clogged, trapping the cerebrospinal fluid within the ventricles, the

pressure of this fluid inside the brain will gradually destroy the tissue there. Or a blood vessel in the meninges covering the brain may rupture and the pressure of the accumulated blood destroy parts of the brain. Tumors and infectious diseases, such as syphilis, can damage the tissue; the actual symptoms—paralysis, loss of sensation or other functions—depend on the part of the brain affected.

The cause of other types of disorder, the so-called functional disorders —neuroses and psychoses—is more baffling, for they occur without any structural or chemical change in the brain which pathologists have so far been able to detect. Typically, these involve emotional disturbances rather than changes in intelligence.

Neuroses are comparatively mild and common disorders with a great variety of symptoms: anxiety, fear, shyness and oversensitiveness. The emotional upsets may actually produce organic disorders, such as irregular heart beat or digestive disturbances. The cause of this type of mental disorder is not positively known, and there is evidence for believing that it differs from person to person, and is complex in every instance. One theory states that neuroses are due to deep-seated conflicts, and in some cases this would seem to be a reasonable explanation. Usually, however, heredity, present environment, past experience and general health all play a part in causing the condition. In any event, the patient is often completely unaware of the cause or causes of his unhappiness. There is no single cure for the various neuroses; many of them respond to the method of psychoanalysis, by means of which the reason for the sense of guilt, conflict or fear is brought to the patient's attention. Other neuroses disappear gradually for no apparent reason, others become increasingly worse, and a few develop into the more serious psychoses.

Psychoses are the severe mental diseases which usually require hospitalization. There are three main types of psychoses, each of which represents an exaggeration of normal tendencies. The manic-depressive psychosis is characterized by an alternation of excessive elation and depression, sometimes accompanied by delusions and hallucinations. Most manic-depressives are normal for most of their lives, but suffer recurrent episodes of insanity. **Paranoia** is a psychosis characterized by delusions, typically of grandeur or persecution. **Dementia praecox** or **schizophrenia** is marked by a withdrawal from the everyday world into a world of daydreams which becomes the world of reality.

Psychoses are much more difficult to cure than neuroses, and most of them are not permanently curable. One of the most drastic therapeutic methods is the shock treatment, based on the theory that psychoties actually can be jolted back into sanity. With this idea in mind, many psychiatrists inject large amounts of insulin or metrazol into the patient, or apply electric currents, all of which have a violent, fit-producing effect on the nervous system. The drawbacks to such treatments are many, and the neural mechanism underlying the results are not clearly understood, but a number of cases have been cured by some variation of the shock treatment.

8. The Peripheral Nervous System. Emerging from the brain and spinal cord and connecting them with every receptor and effector in the

body are the paired cranial and spinal nerves; these make up the peripheral nervous system. Cranial and spinal nerves are made of bundles of nerve fibers, the axons and dendrites. The only nerve cell bodies present in the peripheral nervous system are those of the sensory neurons, aggregated into clusters known as **ganglia,** near the brain or spinal cord, and of certain motor neurons of the autonomic system which will be discussed later.

Cranial Nerves. Twelve pairs of nerves originate in different parts of the brain and innervate primarily the sense organs, muscles and

Table 8. The Cranial Nerves of Man

Number	Name	Origin of Sensory Fibers	Effector Innervated by Motor Fibers
I	Olfactory	Olfactory mucosa of nose (smell)	None
II	Optic	Retina of eye (vision)	None
III	Oculomotor	Proprioceptors of eyeball muscles (muscle sense)	Muscles which move eyeball (with IV and VI); muscles which change shape of lens; muscles which constrict pupil
IV	Trochlear	Proprioceptors of eyeball muscles (muscle sense)	Other muscles which move eyeball
V	Trigeminal	Teeth and skin of face	Some of muscles used in chewing
VI	Abducens	Proprioceptors of eyeball muscles (muscle sense)	Other muscles which move eyeball
VII	Facial	Taste buds of anterior part of tongue	Muscles of the face; submaxillary and sublingual glands
VIII	Auditory	Cochlea (hearing) and semicircular canals (senses of movement, balance and rotation)	None
IX	Glossopharyngeal	Taste buds of posterior third of tongue, lining of pharynx	Parotid gland; muscles of pharynx used in swallowing
X	Vagus	Nerve endings in many of the internal organs—lungs, stomach, aorta, larynx	Parasympathetic fibers to heart, stomach, small intestine, larynx, esophagus
XI	Spinal accessory	Muscles of shoulder (muscle sense)	Muscles of shoulder
XII	Hypoglossal	Muscles of tongue (muscle sense)	Muscles of tongue

glands of the head. The same twelve pairs, innervating similar structures, are found in all the higher vertebrates—reptiles, birds and mammals; fish and amphibia have only the first ten. Like all nerves, these are composed of neurons, although some of them have only sensory neurons (nerves I, II and VIII), some are composed almost completely of motor neurons (III, IV, VI, XI and XII), and the others are made up of both sensory and motor neurons. The names and structures innervated by the cranial nerves are given in Table 8. One of the most important cranial nerves is the **vagus,** which forms part of the autonomic

system and innervates the internal organs of the chest and the upper abdomen.

Spinal Nerves. All the spinal nerves are mixed nerves, having motor and sensory components in roughly equal amounts. In man they originate from the spinal cord in thirty-one symmetrical pairs, each of which innervates the receptors and effectors of one region of the body. Each nerve emerges from the spinal cord as two strands or roots which unite shortly to form the spinal nerve. All the sensory nerves *enter* the cord through the *dorsal root* and all motor fibers *leave* the cord through the *ventral root* (Fig. 128). If the dorsal root is severed, the part of the body innervated by that nerve suffers complete loss of sensation without any paralysis of the muscles. If the ventral root is cut, there is complete paralysis of the muscles innervated by that nerve, but the

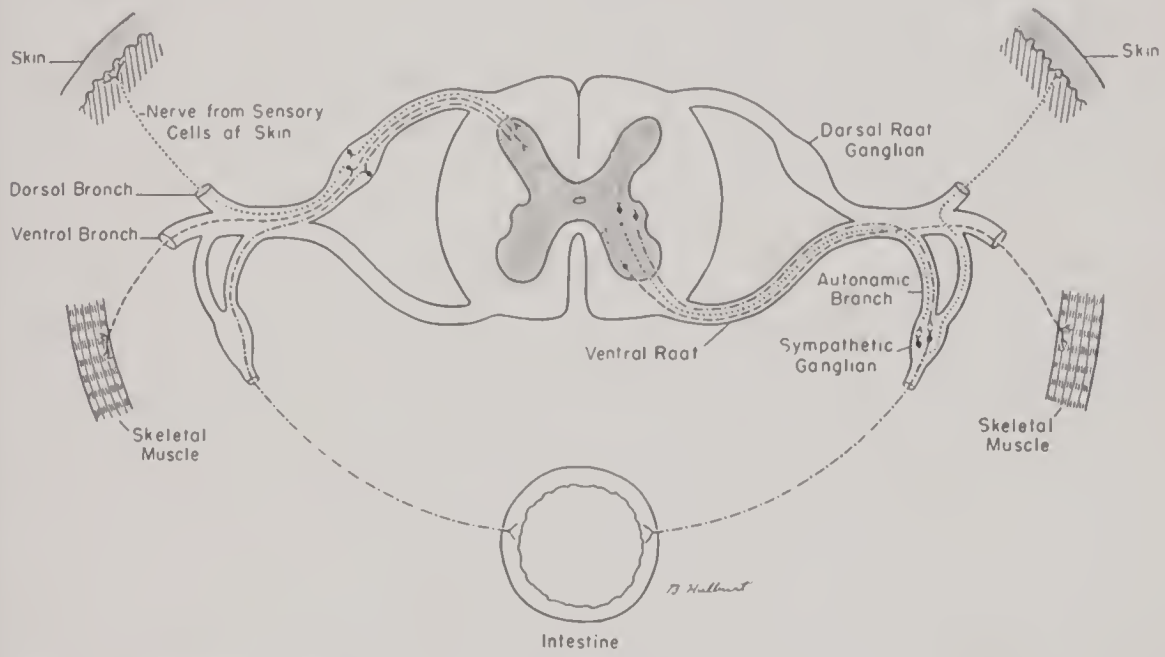


Fig. 128. Diagram of the primary types of sensory and motor neurons of the spinal nerves, and their connections with the spinal cord. For convenience, the sensory neurons are shown on the left and the motor neurons on the right, though both kinds are found on each side of the body.

senses of touch, pressure, temperature, kinaesthesis and pain are unimpaired. The size of each spinal nerve is related to the size of the body area it innervates; the largest in man is one of the pairs supplying the legs. Each spinal nerve, shortly beyond the point of junction of the dorsal and ventral root, divides into three branches: the dorsal branch, serving the skin and muscles of the back; the ventral branch, serving the skin and muscles of the sides and belly; and the autonomic branch, serving the viscera (Fig. 128).

9. Reflexes and Reflex Arcs. A reflex is an inborn, automatic response to a given stimulus depending only on the anatomical relationships of the neurons involved. The neurons which conduct the impulse form a **reflex arc,** the simplest of which is made of one sensory, one connector, and one motor neuron (Fig. 129). Reflexes are the functional units of the nervous system, and most of our activities are the result of them. We have already seen how important reflexes are in controlling heart rate, blood pressure, breathing, salivation, movements of the digestive tract and so forth. When we step on something sharp or come in con-

tact with something hot, we do not wait until the pain is experienced by the brain and then, after deliberation, decide what to do; our responses are immediate and **reflex.** We have begun to withdraw the foot or hand by reflex action before the pain is experienced by the brain. Many of the more complicated activities of our daily lives, such as walking, are regulated to a large extent by reflexes. Those present at birth, and common to all men, are called **inherited reflexes;** others, acquired later as the result of experience, are called **conditioned reflexes.**

Reflexes are classified according to the number of nerve pathways involved. A **simple reflex,** in which stimulation of a sensory nerve produces contraction of a single muscle, is typified by the "knee jerk." When the tendon of the knee cap is tapped, and thereby stretched, receptors in the tendon are stimulated, an impulse travels over the reflex arc up to the spinal cord and down again, and the muscle attached to the tendon contracts, resulting in a sudden straightening of the leg. An important, though fairly simple, reflex is the **flexion** or withdrawal reflex. When an arm or leg is stimulated by anything injurious, the flexor muscles are stimulated and the injured member is pulled away

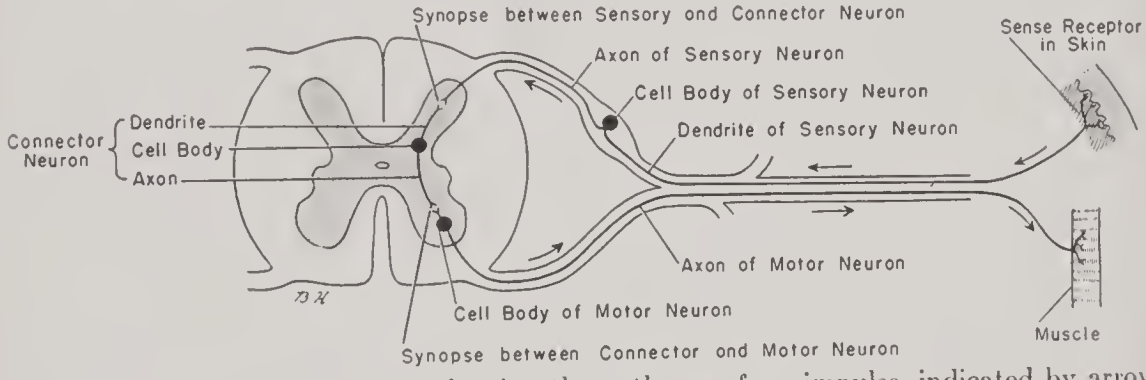


Fig. 129. Diagram of a reflex arc, showing the pathway of an impulse, indicated by arrows.

before further damage occurs. Many reflexes are more complicated than these examples, but even the most complicated of the inherited ones do not require the operation of the higher thought processes. An experiment demonstrating this consists in removing the brain of a frog, while leaving the spinal cord intact, and then applying a piece of acid-soaked paper to the animal's back. No matter how many times the piece of paper is placed on the skin, one leg will invariably come up and flick it away. This response, involving many muscles working in a coordinated fashion, is purely reflex, and clearly demonstrates one of the chief characteristics of a reflex: fidelity of repetition. A frog with a brain might make the response two or three times, but eventually it would do something else—perhaps hop away. Most reflexes have some survival value to the animal; the anatomical configuration responsible for the reflex was selected in evolution because of this survival value.

The behavior of a newborn child is determined largely by its inborn, inherited reflexes; but as he grows older, the relationship between stimulus and response may be altered, and a new stimulus substituted for the old one in eliciting a response. The relationship of new stimulus and old response is known as a **conditioned reflex.** These are usually complicated, indirect and difficult to investigate. The classical investigations of the Russian physiologist, Pavlov, on conditioned reflexes associated

with salivation have made a beginning toward an explanation of the mechanisms involved, and have shown how much learned behavior is built upon inborn behavior.

Normally, saliva is secreted reflexly only when food is in the mouth, but if another stimulus, such as the ringing of a bell, occurs every time food is eaten, a conditioned reflex is established and saliva flows when the bell is rung, whether or not food is present. The ability to form conditioned reflexes is related to the development of the cerebral cortex and is greater in mammals and birds than in lower vertebrates, and almost lacking in invertebrates. If the cortex is removed, the animal loses all his previously acquired conditioned reflexes and the ability to form new ones. It is believed that the formation of conditioned reflexes occurs in the association areas of the cortex. Here, impulses from receptors all over the body converge and are shunted onto motor neurons. The passage of one impulse across a synapse tends to lower the synaptic resistance, so that the impulse from the new stimulus follows the path of the impulse in the previously established reflex; then, by facilitation through repetition, the new pathway becomes established. One conditioned reflex may serve as the basis for another, until ultimately a complex, many-layered series of conditioned reflexes is acquired.

10. Habit, Memory and Learning. Both habit and learning depend to a large extent on the setting up of conditioned reflexes, and these, together with memory, depend upon the fact that a series of impulses passing across the synapses of a given chain of neurons results in a lasting increase in the chain's ability to conduct subsequent impulses. This phenomenon, known as **facilitation,** increases as the synapses continue to be used, until a maximum is reached. The amount of repetition necessary to reach the maximum—really the ability of the animal to "learn"—varies in different species and in different members of the same species. Facilitation is gradually lost if the particular synaptic pathway is not used for a long time; this is the basis for forgetting and loss of habit.

Learning is a complex and poorly understood process that depends on other cerebral activities than the formation of conditioned reflexes. Certain experiments, such as those in which animals learn to run a maze or labyrinth to get food or to avoid electric shocks, have emphasized the role of "trial and error" in learning. The higher mammals, apes and men, show, in addition, the phenomenon of "insight" or getting the idea. After a few random trials, the subject of the experiment sees the point of the problem, and thereafter performs with invariable success.

The experiments demonstrating that particular functions are localized in particular regions of the cortex suggest that at least a few kinds of learning are localized. But the work of Dr. Lashley on learning in rats has indicated that this is not so. Learning, it seems, is a function of the cortex as a whole. By removing parts of the brain and then testing the ability of the rat to learn, he found that the important thing was not which particular areas were left, but the *total amount* of the cortex remaining. The ability to learn appeared to be proportional to the amount of cortex left in the brain, regardless of where the cortex was located. Whether this is true of the human brain is not known.

11. Moods and Emotions. Such phenomena as moods, emotions and personality as a whole also depend on the activity of the cerebral cortex, but the neural mechanisms underlying them are not understood. These, as well as other activities of the higher centers of the brain, are influenced greatly by the conditions of the body; the state of mind can be markedly affected by the state of the stomach. The secretions of several endocrine glands also affect the functioning of the brain; for example, many women have periods of mental depression just before and during menstruation, and it is quite common for the menopause (the period from forty to fifty years of age when the recurring menstrual cycle ceases) to be accompanied by profound emotional and mental disturbances.

In spite of the fact that much is still unknown concerning the whole range of higher mental faculties, including intelligence, personality, character and will, studies in physiology, neurology and endocrinology have uncovered evidence of great value for the problems of everyday life. One conclusion seems obvious: if happiness is a state of mind, it is one over which we have little control. This thing is true also of other attributes of mind: honesty, aggressiveness, perseverance, generosity, and so forth. The insane and feeble-minded are not the only ones who are "not responsible"; we all are only as "good" as our glands, nerves and brain cells allow us to be.

II. THE AUTONOMIC NERVOUS SYSTEM

The internal organs—heart, lungs, digestive tract, glands, and so on—are innervated by a special set of peripheral nerves, collectively called the **autonomic nervous system.** This system in turn is composed of two parts: the **sympathetic** and the **parasympathetic** nerves.

The autonomic system as a whole contains both sensory and motor nerves, but is distinguished from the rest of the nervous system by several features. There is no willful control by the cerebrum over these nerves; we cannot voluntarily speed up or slow down the heart beat or the action of the muscles of the stomach or intestines. Secondly, there is less direct connection between the sensory fibers and the cerebrum, so that the normal stimulation of these fibers does not result in sensations. Another important characteristic of the autonomic system is that each internal organ receives a *double* set of fibers, one set coming via

Table 9. Actions of the Autonomic System

Organ Innervated	Action of Sympathetic System	Action of Parasympathetic System
Heart	Strengthens and accelerates heart beat	Weakens and slows heart beat
Arteries	Constricts arteries and raises blood pressure	Dilates arteries and lowers blood pressure
Digestive tract	Slows peristalsis, decreases activity	Speeds peristalsis, increases activity
Urinary bladder	Relaxes bladder	Constricts bladder
Muscles in bronchi	Dilates passages, makes for easier breathing	Constricts passages
Muscles of iris	Dilates pupil	Constricts pupil
Muscles attached to hair	Causes erection of hair	Causes hair to lie flat
Sweat glands	Increases secretion	Decreases secretion

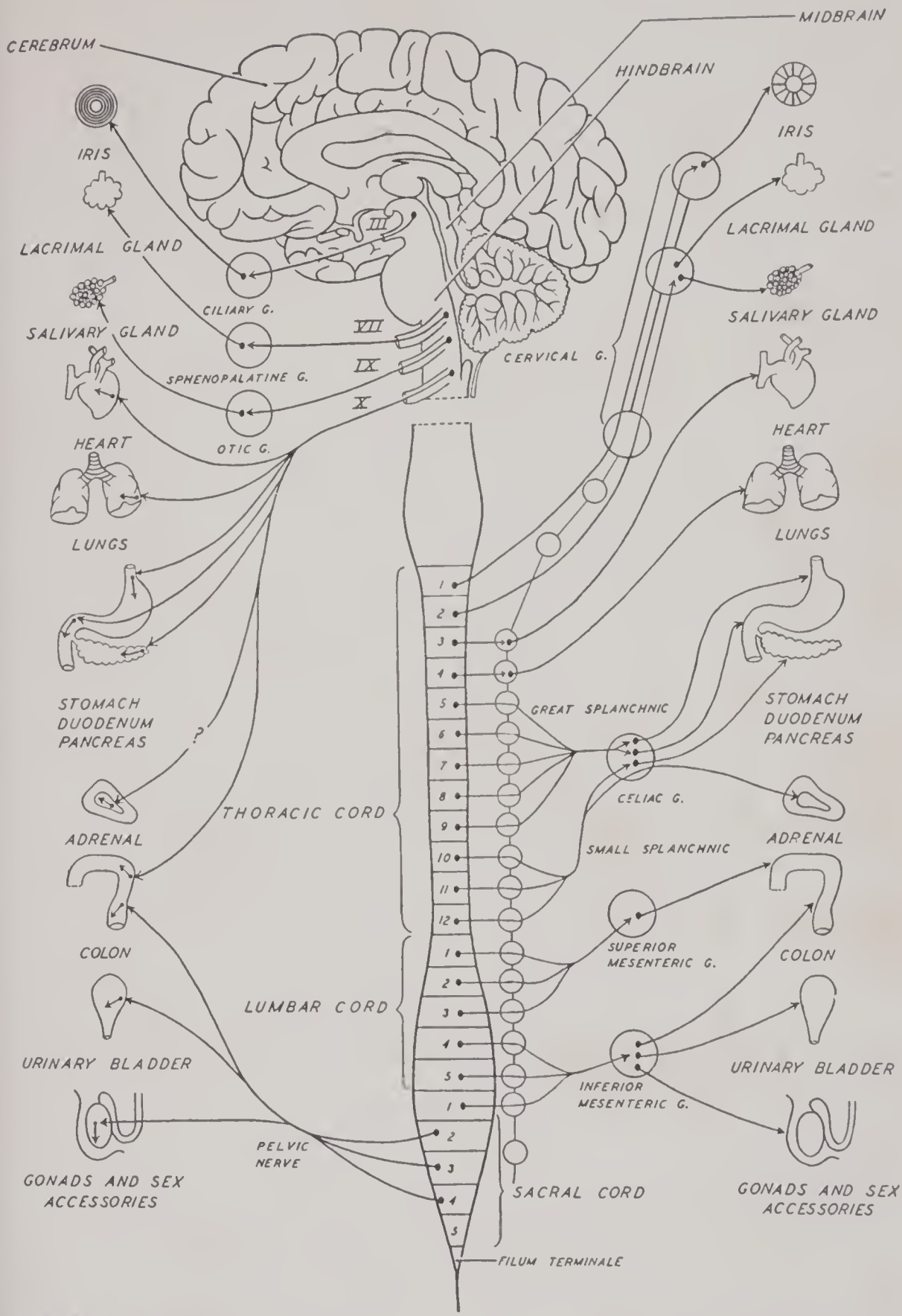


Fig. 130. Diagram of the autonomic nervous system. The parasympathetic system is shown on the left, the sympathetic system on the right. Roman numerals refer to the numbers of the cranial nerves. (Turner, C. D.: General Endocrinology.)

the sympathetic nerves and one set via the parasympathetic nerves. Impulses from the sympathetic and parasympathetic nerves always have antagonistic effects on the organ innervated. Thus, if one speeds up an activity, the other decreases it. These effects are summarized in Table 9.

Still another peculiarity of the autonomic system is that the motor impulses reach the effector organ from the brain or spinal cord, not by a single neuron, as do those to all other parts of the body, but by a *relay* of two or more neurons. The cell body of the first neuron in the set, or chain, is located in the brain or spinal cord; that of the second neuron is located in a ganglion somewhere outside the central nervous system. The ganglia of the sympathetic nerves are close to the spinal cord; those of the parasympathetic nerves are close to, or actually within, the walls of the organs they innervate.

12. The Sympathetic System. The sympathetic system consists of nerve fibers whose cell bodies are located in the lateral portions of the gray matter of the spinal cord. Their axons pass out through the ventral roots of the spinal nerves, in company with the motor neurons to the skeletal muscles, and then separate from these and become the autonomic branch of the spinal nerve going to the sympathetic ganglion. These ganglia are paired, and there is a chain of eighteen of them on each side of the spinal cord from the neck to the abdomen (Fig. 130). In each ganglion the axon of the first neuron synapses with the dendrite of the second neuron. The cell body of this second neuron is located within the ganglion, and its axon passes to the organ innervated. In addition to the fibers going from each spinal nerve to each ganglion, there are fibers passing from one ganglion to the next. The axons of some of the second neurons pass from the sympathetic ganglion back to the spinal nerve and through it to innervate sweat glands, the muscles that make the hair stand erect, and the muscles in the walls of blood vessels. The axons of other second neurons pass from the sympathetic ganglia of the neck up to the salivary glands and the iris of the eye. The sensory neurons (fibers) of the sympathetic system are located within the same nerve trunks as the motor neurons, but enter the spinal cord by way of the dorsal root, together with other sensory nerves of the nonautonomic system.

13. The Parasympathetic System. The parasympathetic system consists of fibers originating in the brain and emerging via the third, seventh, ninth and especially the tenth or vagus nerves, and of fibers originating in the pelvic region of the spinal cord and emerging by way of the spinal nerves in that region (Fig. 130). The vagus nerve arises from the medulla and passes down the neck to the chest and abdomen, innervating the heart, respiratory system and digestive tract as far as the small intestine. The large intestine and the urinary and reproductive systems are innervated by parasympathetic nerves from the pelvic spinal nerves; while the iris of the eye, the sublingual and submaxillary glands and the parotid gland are innervated by the third, seventh and ninth cranial nerves, respectively. These nerves all contain the axons of first neurons in the chain; the ganglia of the parasympathetic system are located in or near the organs innervated, so that the axons of the second neurons are all relatively short.

III. THE NERVOUS SYSTEMS OF LOWER ANIMALS

The unicellular animals, such as the ameba and paramecium, have no neurons, since their entire body consists of but one cell. The ameba does very well without any structure for integration, but the paramecium, whose body is covered with thousands of tiny cilia, needs some mechanism to coordinate the beating of these cilia so that it can move. This is accomplished by a system of tiny fibers, called neuromotor fibers, which stretch from the anterior end of the animal to all the cilia. By a surgical operation performed under the microscope these fibers have been severed, and thereafter the cilia no longer beat in a coordinated fashion, but at random.

The lowest multicellular animals, the sponges, have no nervous system, either; specialized nerve cells are first found in the hydra and other coelenterates. The nerve cells of these animals are not separated from each other by synapses, and associated to form a true system, but are arranged either as separate branched cells or as a nerve net, composed of many cells whose branched processes connect, so that an impulse starting in one part of the body can spread in all directions to every part. There is no differentiation of the neurons of a hydra into sensory, connector and motor types, but some of the branches of the nerve net go to receptor cells, while others go to contractile cells. The amount of response in a hydra depends on the strength of the stimulus: a faint needle prick to a tentacle may cause that single tentacle to roll up, but a stronger prick will cause all the tentacles and the trunk to contract as the animal draws itself into a ball.

Most of the invertebrates have a highly centralized nervous system. This is especially true of the arthropods (the insects, spiders, crabs and lobsters), the molluses (squids and snails), and the annelids, or earthworms. The earthworm has a true nervous system with axons and dendrites arranged in definite nerve cords and fibers. There is a differentiation into central and peripheral systems with separate sensory, connector and motor neurons joined by synapses so that nerve impulses can travel in one direction only. This permits the central nervous system to act as an integrator, selecting certain incoming sensory impulses and passing them on to effectors, while inhibiting or suppressing others. The earthworm has a central nerve cord which runs the entire length of the body, enabling its separate segments to move in a coordinated fashion. The most anterior part of the cord is an enlargement sometimes referred to as the "brain," which sends impulses down the cord to coordinate movements. After removal of this "brain," the animal can move almost as well as before, but it persists in futile efforts to go ahead, instead of turning aside, when it comes to some obstacle. The "brain," therefore, is necessary for adaptive movements. The nervous systems of the other higher invertebrates are rather similar to that of the earthworm. In all, the nerve cord is ventral to the digestive system and is solid.

In the vertebrates the nerve cord is dorsal to the digestive system and is hollow, with a central cavity. The nervous systems of all the vertebrates are fundamentally alike; differences are primarily those of

development of the various brain regions, and in the size of the brain relative to the spinal cord.

IV. THE TRANSMISSION OF IMPULSES IN PLANTS

All living cells, whether animal or plant, exhibit irritability to some extent and can transmit an excitation, even though only slowly. A fertilized egg propagates the excitation produced by the penetration of the sperm at a rate of about 1 cm. per hour, and the unspecialized cells of sponges transmit excitations at the rate of about 1 cm. per minute. The protoplasm of plant cells also can transmit excitations, although usually the rate of propagation is so slow that the results are not easily observed. In a few plants, however, responses to stimuli do occur

Fig. 131. *A*, The sensitive plant, *Mimosa pudica*, before being disturbed. *B*, The plant five seconds after being touched; note how the leaves have folded and drooped. (Courtesy of the General Biological Supply House, Chicago.)

rapidly enough to be easily seen. One of these is the response of the Venus fly trap (p. 32) to the presence of an insect on the leaf, and another is the response of the "sensitive plant" *Mimosa pudica* to touch (Fig. 131). Normally, the leaves of the latter plant are horizontal, but if one of them is lightly touched, all the leaflets fold within two or three seconds. Touching one leaf sharply causes not only the stimulated leaf, but also the neighboring leaves, to fold and droop. After a few minutes the leaves return to their original position. The wilting is due to a change in the turgor pressure of the cells at the base of the leaf, but the excitation is transmitted along the sieve tubes of the leaves and stems. The rate of transmission in *Mimosa* is about 2 inches per second, compared to several hundred feet per second in the nerves of the higher vertebrates, but the nature of the impulse is fundamentally the

same. The excitation is accompanied by electrical phenomena, increased permeability of the excited cells and a temporary change in their metabolism. The response can be altered by various drugs.

Plant cells, then, as well as animal cells, are irritable and can transmit impulses; the nerve cells of animals differ primarily in being specialized for their function, which enables them to conduct impulses more rapidly.

QUESTIONS

1. What are the primary functions of the nervous system?
2. Differentiate between neurons and nerves.
3. How many kinds of neurons are there, and what functions does each type perform?
4. What is the evidence for the theory that the neurilemma sheath plays some part in nerve regeneration?
5. Discuss the nature of the nervous impulse.
6. Is the nervous impulse stimulated in the eye by a beam of light the same as that stimulated in the skin by a hot poker?
7. What are nerve centers, and where are they located?
8. Make a diagram of the brain, labeling the principal parts, and state which functions each part is responsible for.
9. What is a reflex arc?
10. Give an example of a conditioned reflex from your own experience.
11. Explain the term "facilitation."
12. What is the autonomic nervous system? To which of the larger divisions of the entire system does it belong?
13. What light do the facts about the nervous system throw on the old problem of "free will?"
14. Compare the nervous tissue of a hydra and an earthworm.
15. Considering the "All-or-None" Law, how do you explain the fact that a faint needle prick will elicit a small response in a hydra, while a strong prick will cause it to roll into a ball?

SUPPLEMENTARY READINGS

Best, C. H., and Taylor, N. B.: *The Living Body*. New York, Henry Holt & Company, Inc., 1944.
A clear, understandable presentation of human physiology.

Carlson, A. J., and Johnson, V.: *The Machinery of the Body*. 3rd ed. Chicago, University of Chicago Press, 1948.
A well-written and illustrated discussion, on a fairly simple level, of human physiology.

Fulton, J. F.: *Howell's Physiology*. 16th ed. Philadelphia, W. B. Saunders Company, 1949.
One of the standard, detailed, advanced texts of physiology.

Gerard, R. W.: *The Body Functions*. New York, John Wiley & Sons, Inc., 1941.
An interesting account of circulation, digestion and excretion in man.

Pavlov, I. P.: *Conditioned Reflexes*. New York, International Publishers, 1941.
A summary by this classic research worker of his experiments on conditioned reflexes.

Ranson, S. W., and Clark, S. L.: *Anatomy of the Nervous System*. 8th ed. Philadelphia, W. B. Saunders Company, 1947.
A detailed advanced description of the brain and spinal cord.

Sherrington, C.: *The Integrative Action of the Nervous System*. New Haven, Yale University Press, 1947.
An advanced discussion, by one of the foremost neurologists, of the functions of the nervous system.

Zilboorg, G.: *A History of Medical Psychology*. New York, W. W. Norton & Company, Inc., 1941.
An interesting description of the development of psychology and psychiatry.

CHAPTER 17

THE SENSE ORGANS

IN THE discussion of the interrelations between stimulus and response in reflexes, and the phenomenon of irritability common to protoplasm in general, we found that nerve fibers can be stimulated directly by a wide variety of stimuli—electrical, chemical and mechanical. The protoplasm of primitive, single-celled animals, such as the ameba, is sensitive to many different stimuli, as evidenced by the fact that it will move away from bright lights, certain chemicals, electric currents and so forth. But on a higher, more complex level of existence, where the activities of searching for food, attracting a mate, and escaping enemies are correspondingly more complex and hazardous, the animal needs specialized cells sensitive to one or a few types of stimuli, to help him in his struggle for life. In the evolutionary process such receptors have been developed; we call them **sense organs**. As an example of the low thresholds of these receptors, consider that the eye is stimulated by an extremely faint beam of light, while a strong light is required to stimulate the nerve directly. Similarly, the negligible amount of vinegar which can be tasted, or the amount of vanilla which can be smelled, would have no effect at all if applied to the nerve fibers directly.

Traditionally, man is supposed to have five "senses" (i.e., of touch, smell, taste, sight and hearing), but this is misleading, for some of the five can be divided into several completely different senses. Thus, touch, pain, pressure, cold and heat are all included under the sense of touch. In addition, there are more vague and generalized, but none the less important, senses for determining internal states of the body. The receptors for such senses are located in the viscera, the throat, and other places.

Some animals have senses which are lacking in man. For example, recent experiments with pigeons suggest that their sense of direction and perhaps that of other birds as well, depend on stimuli received in some way from the magnetic fields of the earth. Bats in flight continuously make high frequency sounds, inaudible to man and most other animals, which enable them to guide their flight in total darkness, by rebounding as echoes from the obstructions in their paths.

Stimulation of any sense organ initiates what might be considered a coded message, transmitted by the nerve fibers and decoded in the brain. In the transmission of the impulse there may be (1) differences in the number of fibers transmitting, (2) differences in which particular fibers are transmitting, (3) differences in the total number of impulses passing over a given fiber, (4) differences in the frequency of the impulses passing over a given fiber, and (5) differences in the time relations between impulses in different fibers. These, then, are the possibilities in the "code" sent along the nerve fiber; how the sense organ

initiates different codes and how the brain analyzes and interprets them to produce various sensations is still unknown.

1. The Stimulus-Receiving Process. For all types of sense organs the actual excitation of the sensitive cells is either mechanical or chemical. So far as we know, no organism has receptors sensitive to cosmic or radio waves or to electric currents. The stimulation of the touch and pressure receptors of the skin depends on the mechanical stresses transmitted through the surrounding capsules; the proprioceptors (kinesthetic receptors) respond to the mechanical pressure exerted on them when the surrounding muscle cells or tendon fibers are stretched or compressed, and the sensitive cells in the organs of hearing and balance are believed to be excited by ripples or waves in the fluids bathing them. In contrast, the olfactory cells of the nose and the taste buds of the tongue are stimulated chemically by the molecules which come in contact with them. The stimulation of the pain receptors probably depends upon the action of chemical substances released by damaged cells, since they respond to strong stimuli of any sort. The receptors for heat and cold respond to chemical changes induced in them by changes of temperature, and the cells of the retina respond to the chemical reactions which occur when light falls on them.

2. The Perception of Sensations. In considering the problem of the nature of perceptions, it immediately becomes clear that man (or any organism) does not receive a perfectly true and complete picture of his world, or even of himself. In the first place, there are undoubtedly many types of phenomena, a few of which have already been mentioned, for which he has no channel for reception at all; in the second place, even the stimuli for which he is sensitive undergo a "distortion" process in the act of being apprehended. How much of our perception is a product of the sense organs and the brain, and how much is representative of the "real" world, is an interesting philosophical question which we cannot go into here. Most biologists assume that our perceptions do give us a fairly valid picture of our environment; certainly from the survival standpoint, the impressions of a healthy organism are valid. After this assumption our problem is to understand exactly how the external world is translated into our impression of it. It is a difficult task, and much of the answer must remain unknown, at least for the time being.

This much is known, however: whatever awareness we do have is made possible by a "hook-up" between the sense organs and the brain. This connection we call a **nerve impulse**, and it is most important to remember that *all nerve impulses are qualitatively the same.* This means that the impulse instigated by the ringing of a bell is exactly the same as the impulse initiated by the pressure of a pin against the skin, or any other of the countless possible impulses emitted by any sense organ. This being so, it follows that the qualitative differentiation of stimuli must depend upon the sense organ itself, upon the brain, or both. In fact, it depends on both. Primarily, our ability to discriminate red from green, hot from cold, or red from cold, is due to the fact that particular sense organs and their individual sensitive cells are connected to particular parts of the brain.

You can now understand why anesthetics are effective. Since only

those nerve impulses which reach the brain can result in sensations, any blocking of the impulse along the nerve fibers has the same effect as removing the original stimulus entirely. The sense organs, of course, will continue to initiate impulses, which can be detected by the proper electrical apparatus, but the anesthetic prevents them from ever reaching their destination.

3. Localization and Intensity of Stimuli. The localization of stimuli, like the ability to distinguish different qualities of stimuli, depends on the relationship between the sense organ and the part of the brain which it serves. The infant early learns that two sensations, though identical in quality, are associated with stimuli coming from different sides of the body. He is able to localize a bright light in his left eye or a sharp stab in his right side, simply because the nerve fibers from the left eye and the right side have different destinations in the brain from those of the right eye and the left side. It is more difficult to localize odors and still more difficult to localize sounds, since the stimuli for these are more general and diffuse.

The importance of the brain in making sensations possible is emphasized by the phenomenon of "misreference," which occurs occasionally in connection with pain. A well known example of this is the experience of people suffering from gallbladder diseases, who complain of pain in the right shoulder. Actually, of course, the stimulus originates in the gallbladder, but in some as yet not understood way, the nerve impulse ends up in the same part of the brain as impulses genuinely originating in the right shoulder.

In contrast to the quality and localization of stimuli, which depend to such a large extent upon the parts of the brain involved, the intensity of sensation depends almost entirely upon the sense organ initiating the original impulse. This is so because, for almost all sensations, not one but many impulses are sent along the nerve fiber, and it is the number of these which determines how strong the sensation will be. An intense blow will initiate more impulses per second than a light tap, and the greater the area covered by the blow, the stronger the ultimate sensation, since more receptors will be stimulated and more impulses sent.

4. The Tactile Senses. The skin contains several different types of simple sense organs, some of them merely the free ends of dendrites, while others consist of the ends of dendrites enclosed in special cellular capsules (Fig. 132). By making a careful survey of a small area of skin, point by point, using a stiff bristle to test for touch, a hot or cold metal stylus to test for temperature, and a needle to test for pain, it has been found that receptors for each of these sensations are located at different spots. By comparing the distribution of the different types of sense organs and the types of sensations produced, it has been found that the free nerve endings are responsible for pain perception, and that particular types of encapsulated nerve endings are responsible for the others.

5. Kinesthesis. Each muscle, tendon and joint is equipped with nerve endings, called **proprioceptors,** which resemble certain sense organs of the skin. These are sensitive to changes in the tension of the muscle or tendon, and initiate impulses to the brain which are responsible for our awareness of the position and movement of the various parts of the body.

the sense referred to as **kinesthesis.** The existence of this sense enables us, even with our eyes closed, to perform manual acts, such as dressing or tying knots. Impulses from the proprioceptors are also extremely important in insuring the harmonious contraction of different muscles involved in a single movement; without them, complicated, skillful acts would be impossible. These impulses are also important in the maintenance of balance. The proprioceptors are probably more numerous and more continuously active than any of the other senses, although we are less aware of them than of any others; in fact, the existence of this sense was discovered only about a hundred years ago. One obtains some idea of what life without proprioceptors would be like when a leg or arm "goes to sleep"—the feeling of numbness results from the lack of proprioceptive impulses.

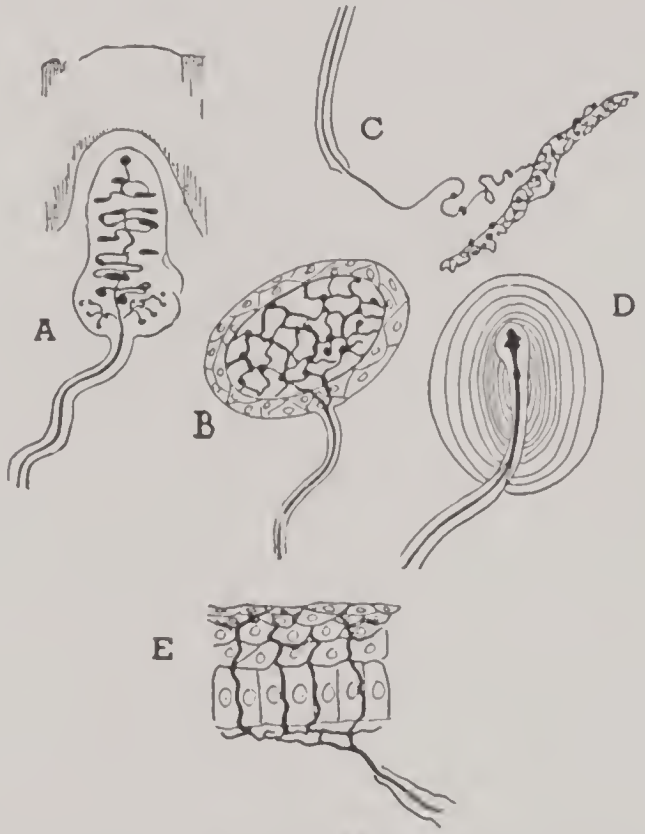


Fig. 132. Sense organs in the skin. *A*, Touch (Meissner's corpuscle); *B*, cold (Krause's end bulb); *C*, warmth (Ruffini's end organ); *D*, deep pressure (Pacinian corpuscle); *E*, pain (bare nerve endings in cornea). (Best and Taylor: The Living Body, Henry Holt & Co., Inc.)

6. Visceral Sensitivity. The sensations associated with the receptors located in the internal organs, which are extremely important in regulating the activities of the viscera, seldom reach the level of consciousness. They bring about reflex control of the functioning of the internal organs by way of reflex centers in the medulla, midbrain or thalamus. A few of the impulses from these receptors do get to the cerebrum, however, and give rise to sensations such as thirst, hunger and nausea. The sensation of thirst originates in receptors in the lining of the throat; when this lining becomes dry, the receptors send impulses to the brain which we interpret as a feeling described as "being thirsty."

The wall of the stomach also contains receptors. When the stomach is empty, a series of strong, slow, muscular contractions sweeps over the walls, stimulating these receptors and resulting in the feeling of hunger.

By having a subject swallow a rubber balloon connected by a tube to a recording device, it was found that hunger pangs were nothing more than these characteristic contractions, Therefore they come and go and return again as the contractions occur. The feeling of nausea also originates from receptors in the stomach, but the contractions responsible for it move up, instead of down the tract as in normal peristalsis.

Still other receptors lie in the mesenteries holding the internal organs in place. When these mesenteries becomes inflamed or stretched by unusual movements of the organs to which they are attached, sensations of pain result. There are other nerve endings for pain in the linings of the organs themselves.

The sense of fullness and the urge to defecate and urinate depend upon receptors in the walls of the rectum and urinary bladder, respec-

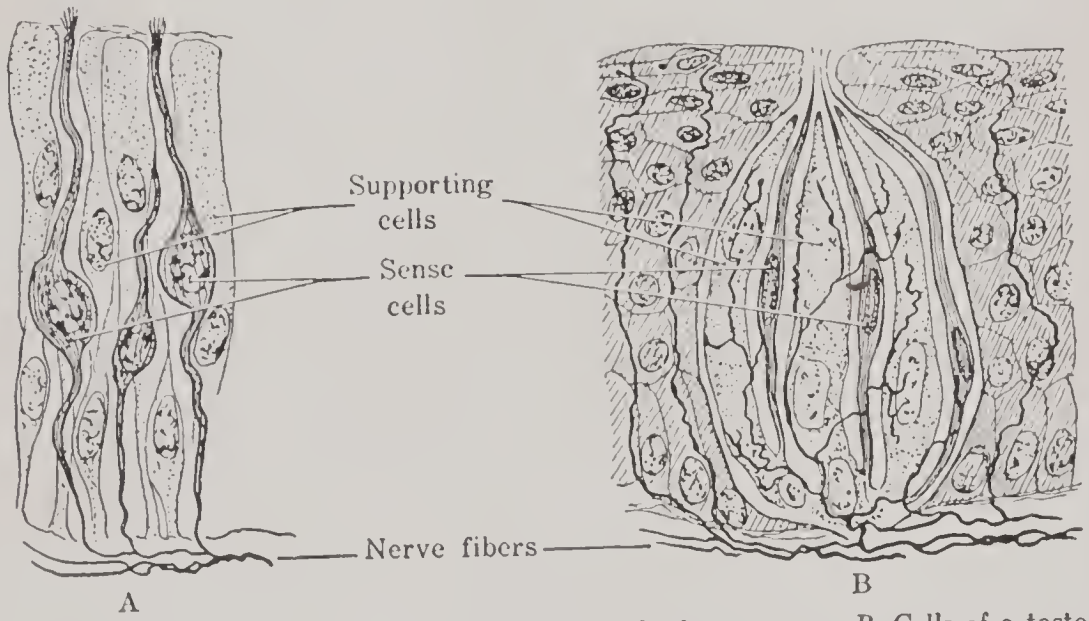


Fig. 133. *A*, Cells of the olfactory epithelium of the human nose. *B*, Cells of a taste bud in the epithelium of the tongue. The external ends of the sense cells are hairlike projections which are activated by chemicals to produce odors and tastes. (Woodruff: Foundations of Biology, 6th Ed., The Macmillan Co.

tively, which are stimulated by the tension resulting when those hollow organs are distended by their contents.

Many other, less well-defined visceral sensations are felt during sexual activity, illness or emotional crises.

7. The Chemical Senses: Taste and Smell. The sensations of taste and smell, important to the animal in obtaining food, are related by the fact that both are stimulated by specific chemical substances. Imbedded in the mucous membranes of the tongue and soft palate are special sense organs known as **taste buds**, each of which consists of a few sensitive cells connected with sensory neurons and surrounded by supporting cells (Fig. 133).* The taste buds open by pores to the surface of the tongue. There are only four basic taste sensations: sour, salt, bitter and sweet, each due to a different kind of taste bud. The buds are distributed unevenly over the surface of the tongue, so that certain parts are espe-

* The restrictions of taste buds to the mouth is not characteristic of all vertebrates; fish, for example, have taste buds all over the outside of their bodies.

cially sensitive to sweet things, others to sour things, and so on.* The taste buds can be stimulated electrically, and when so stimulated produce their characteristic sensation. But the flavor of a substance depends only partly on the sense of taste; the rest is due to the sense of smell. The tiny chemical particles pass from the mouth through the internal nares into the nasal chamber and stimulate the sense organs there. When one has a cold, foods are relatively tasteless because the sense of smell is partly or wholly lost.

There are inherited differences in the sense of taste. Some people find that the chemical phenylthiocarbamide is bitter; others find it tasteless. Ability to taste the chemical is inherited through a single pair of genes.

The sense organs of smell are located in the epithelial lining of the upper part of the nasal cavity in a region not ordinarily washed by the incoming air. Particles entering the nostrils reach them by diffusion and dissolve in the mucus covering the sensitive cells. The sensory cells for smell occur singly and are distinguished from ordinary epithelial cells by hairs which project into the mucous layer (Fig. 133).

In contrast to the sensations of taste, the various odors cannot be classified into definite types; each substance has its own distinctive smell. The olfactory organs respond to remarkably small amounts of a substance. The synthetic substitute for the odor of violets, ionone, can be detected by most people when it is present to the extent of one part in more than thirty billion parts of air. The sense of smell is rapidly fatigued, and air originally having a powerful stimulus may seem odorless after a few minutes. This fatigue is specific for the particular substance producing it, thus receptors that have become insensitive to one substance will react to another quite normally. This suggests that there are many different kinds of sense cells, each specific for a particular chemical. Some people completely lack a sense of smell, while others are able to smell some substances, but not all.

8. Vision. Light-sensitive cells exist in almost all living matter; even protozoa, which lack any special organ, respond to changes in light intensity, usually moving away from the source of light. Most plants orient their leaves and flowers toward the sun, although they have no special light-sensitive structures. In most of the higher animals this light-sensitivity is localized in certain cells and is highly developed. The human eye is an excellent example of an extremely sensitive, specialized organ for perceiving light. Recent experiments by Dr. Hecht and his collaborators at Columbia University have shown that a well dark-adapted eye can detect as little as 6 to 10 quanta of light.†

Some protozoa have "eye spots" which are more sensitive to light than the rest of the cell, but the most primitive light-sensitive organs in the evolutionary scale are those of the flatworms, such as planaria. Their eyes are bowl-shaped structures containing black pigment, at the bottom of which are clusters of light-sensitive cells. These are shaded by

* Salt and sweet tastes predominate at the tip of the tongue, bitter tastes at the base, and sour tastes along the sides.

† Just as matter consists of tiny particles known as atoms, light consists of small corpuscles called photons, and, by definition, the energy of 1 photon is 1 quantum. The light reaching the eye from a candle fourteen miles away is just at the limit of visibility of a normal eye and is about 6 or 7 quanta of light.

the pigment, from light coming from all directions except above and slightly to the front, so that when the animal does become aware of light, it knows from what direction it is coming. These eyes, of course, do not register images as do our eyes, but are merely sensitive to different light intensities. Planaria have other light-sensitive cells over the entire body surface, for they still react to light after their eyes have been removed, though more slowly and less accurately.

Many marine worms have well-developed eyes and other sense organs on the head, but the earthworm, being a burrowing animal, has lost these. It emerges from its burrow at night, however, and the light-sensitive cells on its dorsal surface enable it to recognize the coming of dawn. In addition, the earthworm has cells sensitive to touch and temperature, and to substances placed on its skin and in its mouth and pharynx. Earthworms have definite tastes in food, preferring carrot leaves to celery, and celery to cabbage.

The eyes of insects and crabs are "mosaic" eyes, quite different from the camera eyes of vertebrates. Mosaic eyes are composed of many, sometimes thousands, of visual units, each with a small bundle of light-sensitive cells and a fixed, immovable lens. The action of these eyes does not result in a single, sharp picture as that of a camera eye does, but instead gives a mosaic, to which each unit of the eye contributes a separate image. The effect is imagined to be rather similar to a poor newspaper photograph. Arthropods, then, are not so aware of the details in an image as of the *motion* of objects. Because any movement of prey or enemy is immediately picked up by one of the eye units, this type of organ is peculiarly suited to the arthropod's way of life. Among the invertebrates, only the squid and octopus have camera eyes with lenses that can focus for far and near vision and reproduce reasonably accurate images of the animals' environment.

The Human Eye. The squid or octopus eye is rather like a simple Brownie camera, equipped with slow, black and white film, whereas the human eye is like a de luxe Leica loaded with extremely sensitive color film.

The analogy between the human eye and a camera is complete: the eye (Fig. 134) has a **lens** which can be focused for different distances, a diaphragm (the **iris**) which regulates the size of the light opening (the **pupil**), and a light-sensitive **retina** located at the rear of the eye, corresponding to the film of the camera. Next to the retina is a sheet of cells filled with black pigment which absorbs extra light and prevents internally reflected light from blurring the image (cameras are also painted black on the inside). This sheet, called the **choroid coat,** also contains the blood vessels which nourish the retina.

The outer coat of the eyeball, called the **sclera,** is a tough, opaque, curved sheet of connective tissue which protects the inner structures and helps maintain the rigidity of the eyeball. On the front surface of the eye this sheet becomes the thinner, transparent **cornea,** through which light enters.

Immediately behind the iris is a transparent, elastic ball, the lens, which bends the light rays coming in, bringing them to a focus on the retina. It is aided by the curved surface of the cornea and by the

refraetive properties of the liquids inside the eyeball. The cavity between the eornea and the lens is filled with a watery substance, the **aqueous humor;** the larger chamber between the lens and the retina is filled with a more viscous fluid, the **vitreous humor;** both fluids are important in maintaining the shape of the eyeball. They are secreted by the **ciliary body,** a doughnut-shaped structure which attaches the ligament holding the lens to the eyeball.

The eye accommodates, or changes focus for near or far vision, by changing the curvature of the lens. This is made possible by the stretching and relaxing of the lens by the **ciliary ligament,** which attaches the lens to the ciliary body. Because of the pressure of the fluids within, the eyeball is under tension, whieh is transmitted by the ciliary ligament to the lens. When the lens is stretched, it flattens and focuses the eye for far vision, the condition of the eye at rest. Just in front of the eiliary

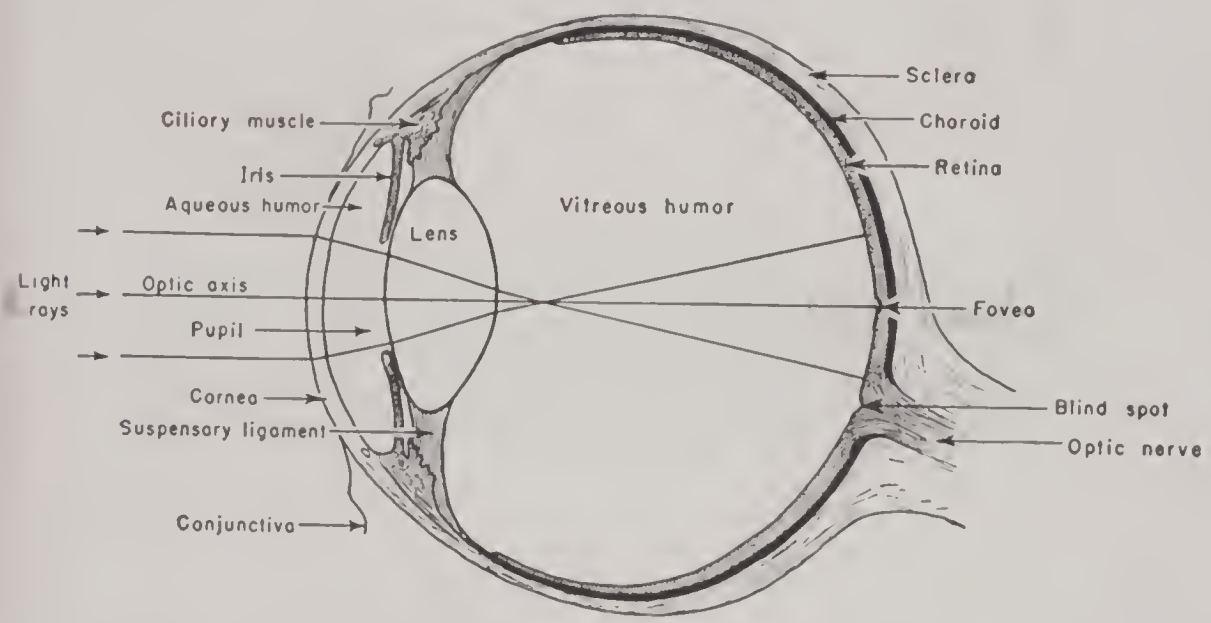


Fig. 134. Horizontal section of the human eye. (Hunter and Hunter: College Zoology.)

body, and attached to the ciliary ligament, are ciliary muscles which, when contracted, take up the strain on the ligament and lens, leaving the latter free to assume the more spherical shape for near vision.

As people grow older, the lens becomes less elastic and thereby less able to accommodate for near vision. When this occurs, spectacles with one part ground for far vision and one for near vision are worn to accomplish what the eye can no longer do.

The amount of light entering the eye is regulated by the iris, a ring of musele whieh appears as blue, green or brown, depending on the amount and nature of pigment present. The structure is composed of two sets of muscle fibers, one arranged circularly, which contracts to decrease the size of the pupil, and one arranged radially, which contracts to increase the size of the pupil. The response of these muscles to changes in light intensity is not instantaneous, but requires ten to thirty seconds; thus when one steps from a light to a dark area, some time is needed for the eyes to adapt to the dark, and when one steps from a dark room to a brightly lighted street, the eyes are dazzled until the size of the pupil is decreased.

Each eye has six muscles stretching from the surface of the eyeball to various points in the bony socket which enable the eye as a whole to move and be oriented in a given direction. These muscles are innervated in such a way that the eyes normally move together and focus on the same area.

The only part of the human eye which is light-sensitive is the retina, a hemisphere made up of an abundance of receptor cells, called, according to their shape, **rods** and **cones**. There are about 125,000,000 rods and 6,500,000 cones. In addition, the retina contains many sensory and connector neurons and their axons. Curiously enough, the sensitive cells are at the back of the retina; to reach them, light must pass through several layers of neurons. There is no logical basis for this, but as the eye develops as an outgrowth of the brain, it folds in such a way that the sensitive cells eventually lie on the farthermost side of the retina. At a point in the back of the eye, the individual axons of the sensory nerves unite to form the optic nerve and pass through the eyeball. Here there are no rods and cones. This area is called the "blind spot," since images falling on it cannot be perceived. Its existence can be demonstrated by closing the left eye and focusing the right one on the + in Figure 135. Starting with the page about 5 inches from the eye, move

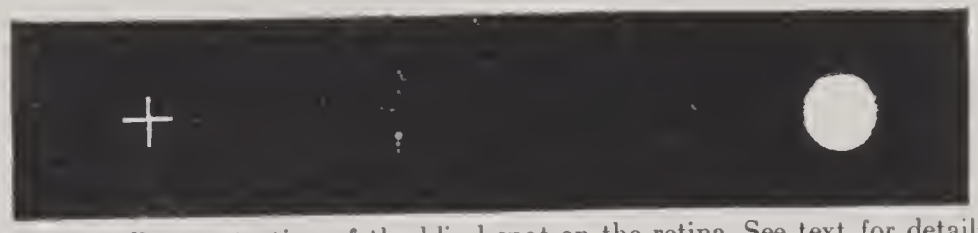


Fig. 135. Demonstration of the blind spot on the retina. See text for details.

it away until the circle disappears. At that position the image of the circle is falling on the blind spot and so is not perceived.

In the center of the retina, directly in line with the center of the cornea and lens, is the region of keenest vision, a small depressed area called the **fovea**. Here the light-sensitive cones, responsible for bright light vision, for the perception of detail and for color vision, are concentrated.

The other light-sensitive cells, the rods, are more numerous in the periphery of the retina, away from the fovea. These function in twilight or dim light and are insensitive to colors. One is not ordinarily aware that color can be perceived only in those objects which are more or less directly in front of the eyes, but the fact can be demonstrated by a simple experiment. If you close one eye and focus the other on some point straight ahead, as a colored object is gradually brought into view from the side, you will be aware of its presence and of its size and shape, before you are aware of its color. Only when the object is brought closer to the direct line of vision, so that its image falls on a part of the retina containing cones, can its color be determined. The rods are actually more sensitive in dim light than are the cones. Since the rods are located not in the center, but in the periphery of the retina, it is a curious fact that you can see an object better in dim light if you do not look at it directly (for then its image will fall on the cones in the center of the retina), but slightly to one side of it, so that its image falls on the rods in the periphery of the retina.

Every rod contains a light-sensitive chemical known as **visual purple,** a compound of vitamin A and a protein. When light falls on the rods, the light energy causes a chemical breakdown of the visual purple to a different chemical known as visual yellow. Each quantum of light falling on the retina causes the breakdown of one molecule of visual purple, which stimulates one rod cell. For a light to be perceived, about six to ten rods have to be excited at once. In the dark, the visual yellow is resynthesized into visual purple, and the rod is ready to be stimulated again. Since visual purple contains vitamin A, a certain amount of that substance is necessary for this synthesis; hence people whose diets are deficient in vitamin A are unable to resynthesize visual purple at an adequate rate and become unable to see in dim light. After thirty to sixty minutes in the dark, the eye becomes adapted and is much more sensitive—perhaps a thousand times more so—than in the light. Although the rods do not function in bright light, some of the visual purple is constantly being broken down as long as the eyes are exposed to it; but when one remains in the dark, all the visual yellow is converted to visual purple, and the eye attains its maximum sensitivity. For this reason, night-flying aviators frequently remain in the dark or wear thick red glasses to dark-adapt their eyes before flying.

Less is understood about the chemistry of the cones, but they are known to contain a substance called **visual violet,** also made of vitamin A plus a protein. A number of theories, none of which is completely satisfactory, have been proposed to explain color vision. It seems likely that there are at least three different kinds of cones, sensitive to three different light wavelengths, which produce the sensations of redness, blueness and greenness. When all are stimulated equally, the sensation of whiteness results. Impressions of intermediate colors, such as orange, result from the simultaneous but unequal stimulation of two or more types.

Defects in Vision. The defects of the eye most common in man are near-sightedness (myopia), far-sightedness (hypermetropia) and astigmatism. In the normal eye (Fig. 136, *A*) the shape of the eyeball is such that the retina is the proper distance behind the lens for the light rays to converge in the fovea. In a near-sighted eye (Fig. 136, *B*) the eyeball is too long, and the retina is too far from the lens, so that the light rays converge at a point in front of the retina, and are again diverging when they reach it, resulting in a blurred image. In a far-sighted eye (Fig. 136, *C*), the eyeball is too short and the retina too close to the lens, causing the light rays to strike the retina before they have converged, again resulting in a blurred image. Concave lenses correct for the near-sighted condition by bringing the light rays to a focus at a point farther back, and convex lenses correct for the far-sighted condition by causing the light rays to converge farther forward.

Astigmatism is a condition in which the cornea is curved unequally in different planes, so that the light rays in one plane are focused at a different point from those in another plane (Fig. 136, *D*). To correct for astigmatism, lenses must be ground unequally to compensate for the unequal curvature of the cornea.

In old age the lens may lose its transparency, become opaque, and

interfere with the transmission of light to the retina, causing blindness. The only cure for this is surgical removal of the lens. This restores sight, but removes the ability to focus, so that a lensless person must wear special spectacles as a substitute for the lens.

The position of the eyes in the head of man and certain other higher vertebrates permits them to focus both eyes on the same object. This

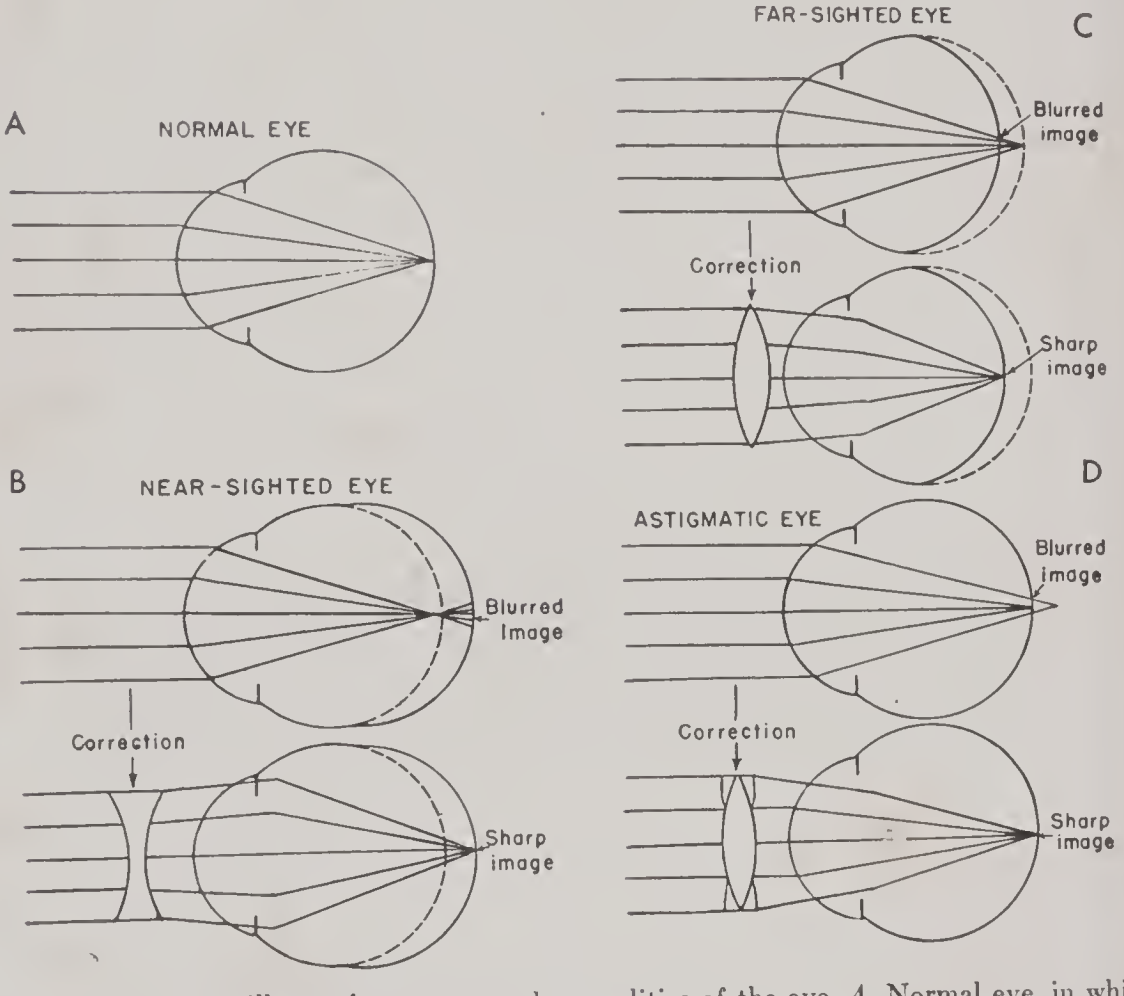


Fig. 136. Diagram illustrating common abnormalities of the eye. *A*, Normal eye, in which parallel light rays coming from a point in space are focused as a point on the retina. *B*, Near-sighted eye, in which the eyeball is elongated so that parallel light rays are brought to a focus in front of the retina (on dotted line, which represents the position of the retina in the normal eye) and so form a blurred image on the retina. This situation is corrected by placing a concave lens in front of the eye. This diverges the light rays, making it possible for the eye to focus these rays on the retina. *C*, Far-sighted eye, in which the eyeball is shortened and light rays are focused behind the retina. A convex lens converges the light rays so that the eye focuses them on the retina. *D*, Astigmatic eye, in which light rays passing through one part of the eye are focused on the retina, while light rays passing through another area of the lens are not focused on the retina, owing to unequal curvature of the lens or cornea. A cylindrical lens will correct this by bending light rays going through only certain parts of the eye. (Hunter and Hunter: College Zoology.)

binocular vision is an important factor in judging distance and depth. To focus on a near object, the eyes must converge (become slightly cross-eyed). In the eye muscles causing this convergence are proprioceptors stimulated by this contraction to send impulses to the brain; hence part of our judgment of distance and depth depends upon impulses which result when the sensory fibers in those muscles are stimulated. In addition, the eyes, being a little over 2 inches apart, see things

from slightly different angles and thus get slightly different views of a close object.

9. The Ear. The organs of two different senses, hearing and equilibrium, are located in the ear. These organs are buried deep in the bone of the skull, and a number of accessory structures are needed to transmit sound waves from the outside to the deep-lying sensory cells. The ear may be divided into outer, middle, and inner parts; by reference to the diagram (Fig. 137) the path of the sound waves may be followed.

The outer ear consists of two parts, the skin-covered cartilaginous flap or **pinna,** and the **auditory canal** leading from it to the middle ear.

The pinnas, or visible ears, are of some slight use in man for directing sound waves into the canal, but in other animals such as the cat, the

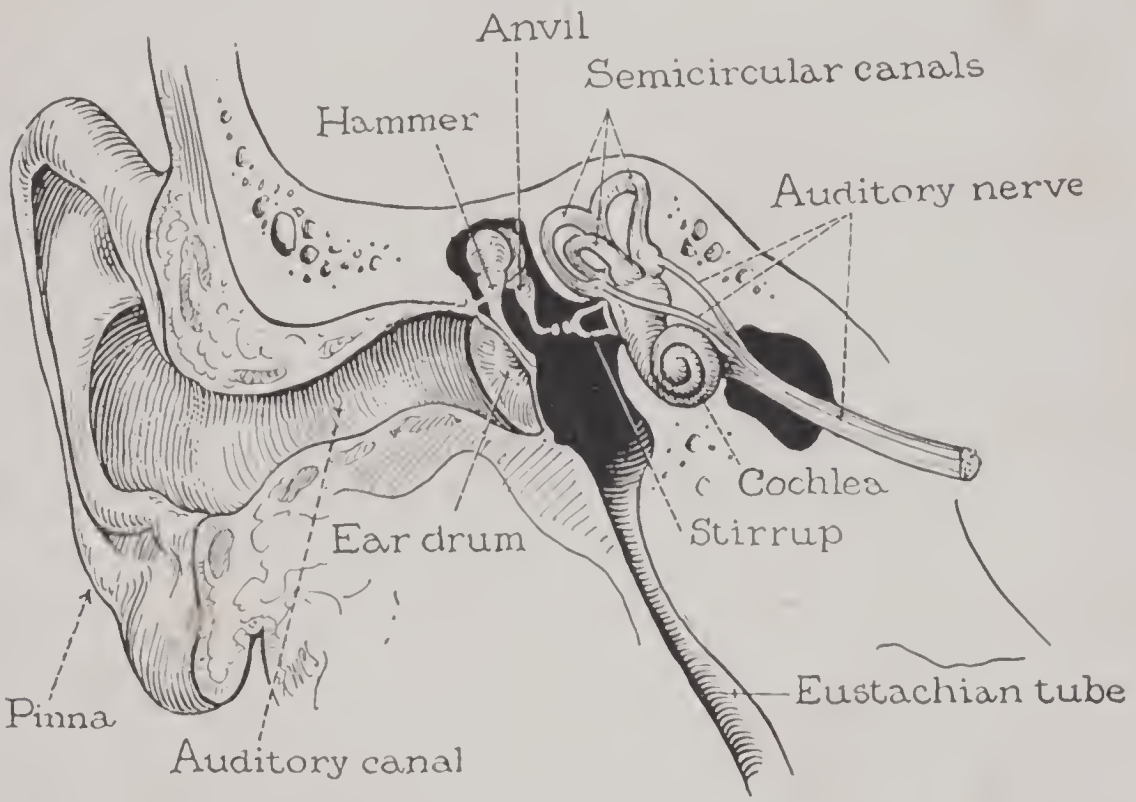


Fig. 137. Structure of the ear, shown schematically. (Clendening, L.: The Human Body. Copyright 1927, 1945, by Alfred A. Knopf, Inc.)

larger, movable pinnas are very important. At the junction of the auditory canal and the middle ear is stretched a thin, connective tissue membrane, the **ear drum,** which the sound waves set vibrating.

The middle ear is a small chamber containing three tiny bones connected in a series, the **hammer, anvil** and **stirrup** (so called because of their shapes), which transmit the sound waves across the middle ear cavity. The hammer is in contact with the ear drum, and the stirrup is in contact with the membrane of the opening into the inner ear, called the **oval window.** The middle ear is connected to the pharynx by the narrow **eustachian tube,** which serves to equalize the pressure on the two sides of the ear drum. If the middle ear were completely closed, any variation in atmospheric pressure would cause a pronounced and painful bulging or caving in of the ear drum. At the pharyngeal end of the eustachian tube is a valve, normally closed, which prevents one from becoming unpleasantly aware of his own voice. This valve

is opened during yawning or swallowing, and during an abrupt ascent or descent in an elevator or airplane such acts help prevent the cracking sensation of the ear drums produced by the changes in atmospheric pressure accompanying changes in altitude. Unfortunately, the eustachian tube also provides a path for organisms which sometimes cause infections resulting in the fusing of the middle ear bones and loss of hearing.

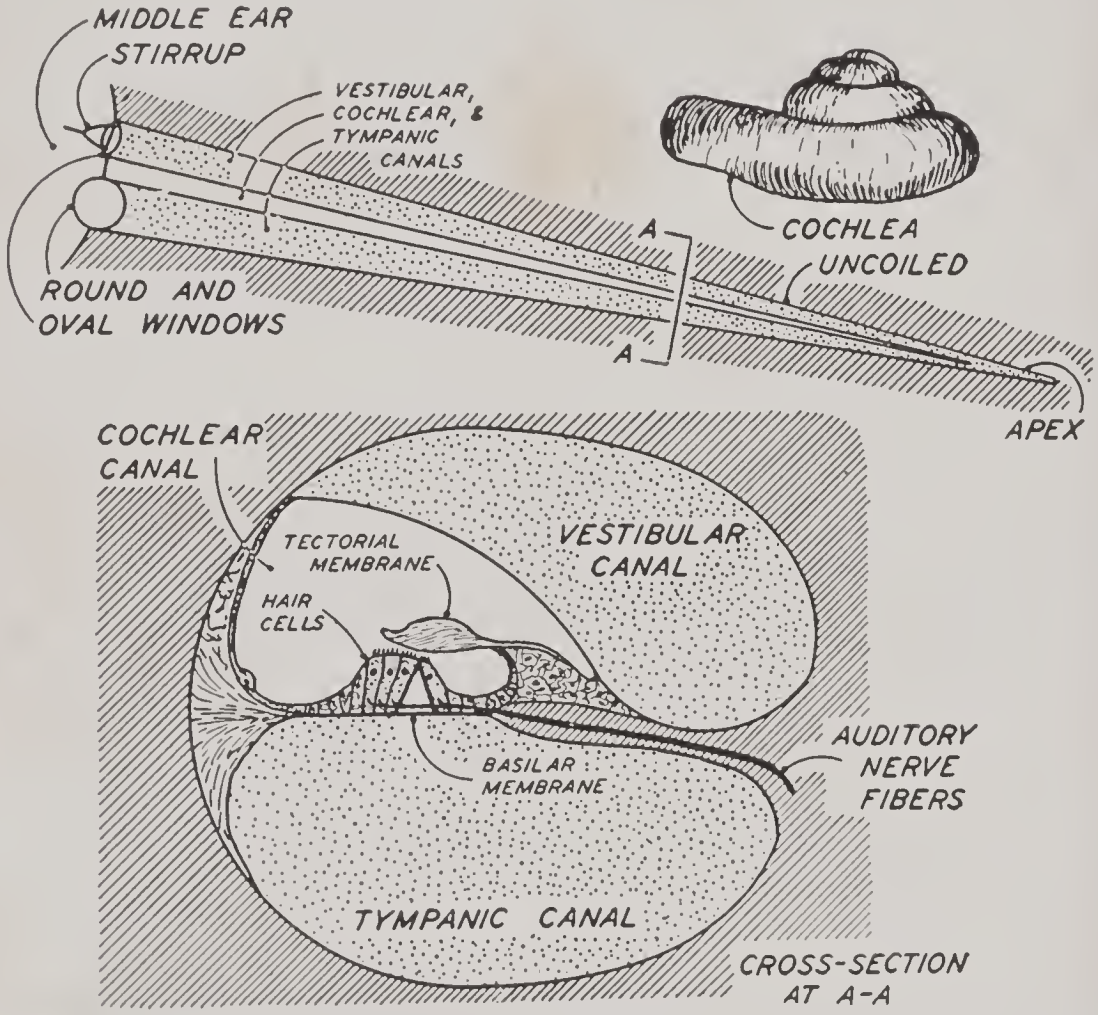


Fig. 138. *Above,* The cochlea—the organ of hearing, shown dissected out of the skull and schematically, as though it were uncoiled and split open, revealing the three canals. Vibrations of the stirrup set the perilymph (shown stippled) in the vestibular canal in motion; the vibrations are transmitted to the basilar membrane and the organ of Corti resting upon it. *Below,* The organ of Corti is shown in cross section through one part of the cochlea. The hair cells, innervated by the branches of the auditory nerve, are the receptor cells for hearing. (Carlson and Johnson: The Machinery of the Body, 3rd Ed., published by University of Chicago Press.)

The inner ear consists of a complicated group of interconnected canals and sacs, often referred to, most appropriately, as the **labyrinth.** The part of the labyrinth concerned with hearing is a spirally coiled tube of two and a half turns, resembling a snail's shell, called the **cochlea.** If the cochlea were uncoiled, as in Figure 138, it could be seen to consist of three canals separated from each other by thin membranes and coming almost to a point at the apex. The oval window is connected to the base of one of these tubes, the **vestibular canal.** At the base of the **tympanic canal** is another opening covered by a membrane, the **round window,** which also leads to the middle ear. These two canals

are connected with each other at the apex of the cochlea and are filled with a fluid known as the **perilymph**. Between the two lies a third, the **cochlear canal**, filled with a fluid called **endolymph** and containing the actual organ of hearing, the **organ of Corti**. This structure consists of five rows of cells with projecting hairs which extend the entire length of the coiled cochlea. Each organ of Corti contains about 24,000 of them. These cells rest upon the **basilar membrane**, which separates the cochlear from the tympanic canal. Overhanging the hair cells is another membrane, the **roof** (or tectorial) **membrane**, attached along one edge to the membrane on which the hair cells rest, and with its other edge free. The hair cells initiate impulses in the fibers of the auditory nerve.

For a sound to be heard, sound waves must first pass down the auditory canal and set the ear drum vibrating. These vibrations are transmitted across the middle ear by the hammer, anvil and stirrup, which are so arranged that they decrease the amplitude, but increase the force, of the vibrations. The stirrup transmits the vibrations, via the oval window, to the fluid in the vestibular canal. Since fluids are incompressible, the oval window could not cause a movement of the fluid in the vestibular canal unless there were an escape valve for the pressure. This is provided by the round window at the end of the tympanic canal. The pressure wave presses upon the membranes separating the three canals, is transmitted to the tympanic canal, and causes a bulging of the round window. The movements of the basilar membrane produced by these pulsations are believed to rub the hair cells of the organ of Corti against the overlying roof membrane, thus stimulating them and initiating nerve impulses in the dendrites of the auditory nerve, lying at the base of each hair cell.

Since sounds differ in pitch, intensity and quality, any theory of hearing must account for the ability to discriminate such differences. Microscopic examination of the organ of Corti reveals that the fibers of the basilar membrane are of different lengths along the coiled cochlea, being longer at the apex and shorter at the base of the coil, thus resembling a harp or piano. It is believed that specific fibers in the basilar membrane are tuned to and set into vibration by sounds of specific pitches. When the ear is subjected to intense, continuous sound, the organ of Corti is injured. This was demonstrated by an experiment on guinea pigs in which the animals were exposed to continuous pure tones for a period of several weeks. When their cochleas were examined microscopically after death, it was found that the guinea pigs subjected to high-pitched tones suffered injury only in the lower part of the cochlea, while those subjected to low-pitched tones suffered injury only in the upper part of the cochlea. Workers, such as boilermakers, subjected to loud, high-pitched noises over a period of years, frequently become deaf to high tones, because of injury of the cells toward the base of the organ of Corti. Recent research indicates that the nerve impulses produced by particular sounds have the same frequency as those sounds, so that the brain may recognize particular pitches by the frequency of the nerve impulses reaching it, as well as by the identity of the nerve fibers conducting the impulses.

The auditory nerves send two kinds of nerve impulses: ordinary nerve

impulses like those of any other nerve, and a different type called **microphonic**. The energy for the latter is not derived from the metabolism of the nerve fiber, as is the energy for the former; instead, the cochlea acts as a microphone to convert the mechanical energy of the sound vibrations into electrical energy. For this reason the wave form of the electrical potential from the cochlea closely resembles that of the stimulating sound wave. In fact, Wever and Bray placed electrodes on the auditory nerve of a decerebrated cat, and then, listening with a telephone receiver to the amplified signals of the nerve, were able to hear not only musical tones, but actual words spoken to the cat. The hair cells of the organ of Corti are believed to be responsible for this conversion of mechanical to electrical energy, the upper and lower ends of the cochlea responding to low and high tones, respectively. It is still a disputed question, however, whether these microphonics have anything to do with the actual sensation of hearing in the normal animal.

The intensity or loudness of a tone depends upon the number of hair cells stimulated. A gentle sound wave does not produce as intense a sensation as a stronger one because it fails to create as great a vibration of the basilar membrane and hence of the individual hair cells.

Variations in the quality of sound, such as are produced when an oboe, a cornet and a violin play the same note, depend upon the number and kinds of **overtones** or **harmonics** present, which stimulate different hair cells in addition to the main stimulation common to all three; thus, differences in quality are recognized by the *pattern* of the hair cells stimulated. Careful histological work has shown that the nerve fibers from each particular part of the cochlea go to a particular part of the auditory area of the brain, so that certain brain cells are responsible for sensations of high tones, others for low tones.

The human ear is equipped to register sounds of frequencies between about 20 and 20,000 cycles per second, although there are great individual differences. Some animals—dogs, for example—can hear sounds of much higher frequencies. The human ear is more sensitive to sounds between 1000 and 2000 cycles per second than to higher or lower ones.* Within this range the ear is extremely sensitive; in fact, when contrasted with the power of light waves necessary to produce a sensation, the ear is ten times more sensitive than the eye.

The normal human ear is just about as efficient a hearing device as anything could possibly be, for, like the eye, it has evolved to the point where any further increase in sensitivity would be useless. If it were more sensitive, it would pick up the random movement of the air molecules, which would result in a constant hiss or buzzing. If the eye were more sensitive, a steady light would appear to flicker because the eye would be sensitive to the individual photons (light particles) impinging on it.

There is little fatigue connected with hearing. Even though it is constantly assailed by noises, the ear retains its acuity and fatigue disappears after a few minutes. When one ear is stimulated for some time by a loud noise, the other ear also shows fatigue—loses acuity—indicat-

* Most human speech sounds lie between 200 and 6000 cycles.

ing, not unexpectedly, that some of the fatigue is in the brain rather than in the ear itself.

Deafness may be caused by injuries or malformations of either the sound-transmitting mechanisms of the outer, middle or inner ears, or of the sound-perceiving mechanism of the latter. The external ear may become obstructed by wax secreted by the glands in its wall; the middle ear bones may become fused after an infection; or, more rarely, the inner ear or auditory nerve may be injured by a local inflammation or the fever accompanying some disease.

Relatively few animals have a sense of hearing. The vertebrate ear began as an organ of equilibrium, the cochlea being a later evolutionary

Fig. 139. The right semicircular canals and cochlea of an adult man, dissected free of the surrounding bone and enlarged five times, as seen from the inner and posterior side. Note that each of the three semicircular canals is perpendicular to the other two. (After Spalteholz, in Maximow and Bloom.)

outgrowth of the saccule which reaches full development only in mammals. The human ear is indeed a curious evolutionary hodgepodge: the cells sensitive to sound are apparently adaptations of cells sensitive to the motion of liquids; the middle ear and eustachian tube were originally part of the respiratory apparatus of fish; the stirrup was originally a structure which attached the jaws of primitive fishes to the cranium, and the hammer and anvil are the remnants of the lower and upper jaws, respectively, of our ancestral fish. In the jawless fish ancestral to these the structures were part of the support for the gills. Thus, respiratory organs became, first, eating organs, and then organs for hearing. This is an example of one of the fundamental patterns of evolution—the reshaping of old organs to perform new functions, rather than the setting up of completely new structures.

Equilibrium. Besides the cochlea, the labyrinth of the inner ear consists of two small sacs—the **saccule** and **utricle**—and three **semicircular canals** (Fig. 139). These structures are filled with endolymph and float in a pool of perilymph. Destruction of them causes a considerable loss of the sense of equilibrium, and a pigeon whose organs have been destroyed is unable to fly. In time he can relearn to maintain equilibrium using visual stimuli.

Equilibrium in man depends upon the sense of vision, stimuli from the proprioceptors, and stimuli from cells sensitive to pressure in the soles of the feet, as well as upon stimuli from these organs in the inner ear. In certain types of deafness the equilibrium organs of the inner ear as well as the cochlea are inoperative, yet the sense of equilibrium remains unimpaired.

The utricle and saccule are small, hollow sacs lined with sensitive hair cells and containing small ear stones or otoliths made of calcium carbonate. Normally, the pull of gravity causes the otoliths to press against particular hair cells, stimulating them to initiate impulses to the brain via sensory nerve fibers at their bases. When the head is tipped, the otoliths press upon the hairs of other cells and stimulate them.

Many invertebrates such as the crayfish and lobster have similar organs. An ingenious experiment was performed to demonstrate the action of these organs in the crayfish; it depended on the fact that as the crayfish moults—sheds its skin and grows another, larger one—it also develops new organs of equilibrium and supplies them with grains of sand picked up from the environment. By supplying the moulting crayfish with particles of iron, the experimenters caused the animals to respond to a magnet. When the magnet was placed directly over the animal, pulling the iron filing against the hair cells on the top of its equilibrium organ, the crayfish thought that "up" was "down" and responded by turning over and swimming on its back.

The labyrinth of each ear has three semicircular canals, each of which consists of a semicircular tube connected at both ends to the utricle. The canals are so arranged that each is at right angles to the other two. At one of the openings of each canal into the utricle is a small, bulblike enlargement containing a clump of hair cells similar to those in the utricle and saccule, but lacking otoliths. These cells are stimulated by movements of the fluid (endolymph) which fills the canals. When the head is turned, there is a lag in the movement of the fluid within the canals, so that the hair cells in effect move in relation to the fluid, and are stimulated by its flow. This stimulation produces not only the consciousness of rotation, but certain reflex movements in response to it, movements of the eyes and head in a direction opposite to the original rotation. Since the three canals are located in three different planes, a movement of the head in any direction will stimulate the movement of the fluid in at least one of the canals. By irrigating the canal of the outer ear with warm or cold water, convection currents can be set up causing movements in the fluid of the canals without movement of the head. Sensations of rotation and dizziness result. Man has become used to movements in the horizontal plane, which stimulate certain semicircular canals, but he is unused to vertical movements parallel to the

long axis of the body. Such movements—the motion of an elevator or of a ship pitching in a rough sea—stimulate the semicircular canals in an unusual way and, for some unknown reason, produce the sensation of nausea and the vomiting of sea or motion sickness. When one lies down, the movement stimulates the semicircular canals in a different way, and nausea is less likely to occur.

QUESTIONS

1. Define proprioceptors, and explain what they do.
2. Draw a diagram of the eye, labeling all the parts, and explain the mechanics of how light rays stimulate the receptors.
3. Explain the role of visual purple in sight.
4. What causes myopia? hypermetropia? astigmatism?
5. Explain how the eye is regulated for near and far vision and for seeing in bright and dim lights.
6. Draw a diagram of the ear, labeling all the parts. Explain the mechanics of how sound waves stimulate the sensory cells of the ear.
7. What are otoliths, and what is their role in maintaining equilibrium?
8. The philosopher Berkeley, as well as many others, believed that there is no material world independent of our sense perceptions, but that what we call perceptions of the external world are really *ideas* transferred from God's mind to our own. Do you think there are any facts in this chapter which absolutely disprove this theory? If you decide there are not, can you think of any other facts which disprove it?
9. Do you think there is justification for the often-repeated statement that one person's taste is as good as another's? If not, what do you think is or should be the basis for esthetic judgement? Could there be such standards completely independent of the human race? of *any* conscious, perceptive organisms?

SUPPLEMENTARY READINGS

Bartley, S. H.: *Vision*. New York, D. Van Nostrand Company, Inc., 1941.
A detailed but understandable presentation of the structure and function of the eye.

Best, C. H., and Taylor, N. B.: *The Living Body*. New York, Henry Holt & Company, Inc., 1944.
A clear, understandable presentation of human physiology.

Carlson, A. J., and Johnson, V.: *The Machinery of the Body*. 3rd ed. Chicago, University of Chicago Press, 1948.
A well-written and illustrated discussion, on a fairly simple level, of human physiology.

Fulton, J. F.: *Textbook of Physiology*. 16th ed. Philadelphia, W. B. Saunders Company, 1949.
One of the standard, detailed, advanced texts of physiology.

Gerard, R. W.: *The Body Functions*. New York, John Wiley & Sons, Inc., 1941.
An interesting account of circulation, digestion and excretion in man.

Stevens, S. S., and Davis, H.: *Hearing, Its Psychology and Physiology*. New York, John Wiley & Sons, Inc., 1938.
A comprehensive discussion of the sense of hearing.

CHAPTER 18

THE ENDOCRINE SYSTEM

THE human body is equipped with two main sets of controls which regulate the activities of the whole organism. One of these is the nervous system; the other is a group of hormone-secreting glands, collectively called the **endocrine system.** The basic difference between nervous and hormonal control is in the speed with which they effect changes. By means of the nervous system an organ can undergo extremely rapid adaptation to changes in the environment. In contrast, hormonal regulation is much slower, but longer lasting. You are already familiar with a typical example of its effects, from the discussion of the stimulation of the flow of pancreatic juice from the pancreas by the hormone **secretin,** manufactured by cells in the lining of the intestine (see p. 210).

The endocrine glands are distinguished by the fact that they secrete substances into the blood stream, rather than into a duct leading to the outside of the body or to one of the internal organs. For this reason they are sometimes referred to as ductless glands or glands of internal secretion. Some glands—the thyroid, parathyroids, pituitary and adrenals—function only in the secretion of hormones and are strictly ductless glands. Others, such as the pancreas, ovaries and testes, have both external secretions, via ducts, and internal secretions, carried by the blood stream. The pancreas, which is really two functionally separate organs combined in the same structure, produces digestive enzymes as well as a hormone. In some of the lower animals the two parts of the pancreas are anatomically separate.

Hormones cannot be defined as belonging to any particular class of chemicals. All hormones are organic substances, but some are proteins, while others are much simpler chemicals, such as amino acids or steroids. The distinguishing factor about them all is that they are secreted by cells in one part of the body and carried by the blood stream to some other part where they regulate the activities of the cells. All the hormones, and of course the glands secreting them, are necessary for the normal functioning of the body; a deficiency or an oversecretion of any one produces a characteristic pathological condition. These are frequently called **functional diseases** to distinguish them from deficiency diseases caused by the lack of vitamins, and from infectious diseases, caused by the presence of some infective agent such as a bacterium.

Practical knowledge of endocrinology—exemplified by the castration of both men and animals—has existed for several thousand years, but modern endocrinology usually is said to date from 1889. At that time the famous French scientist Brown-Séquard, feeling old and debilitated, injected himself with testicular extracts and claimed that the injections were beneficial and rejuvenating. It is uncertain whether the extracts

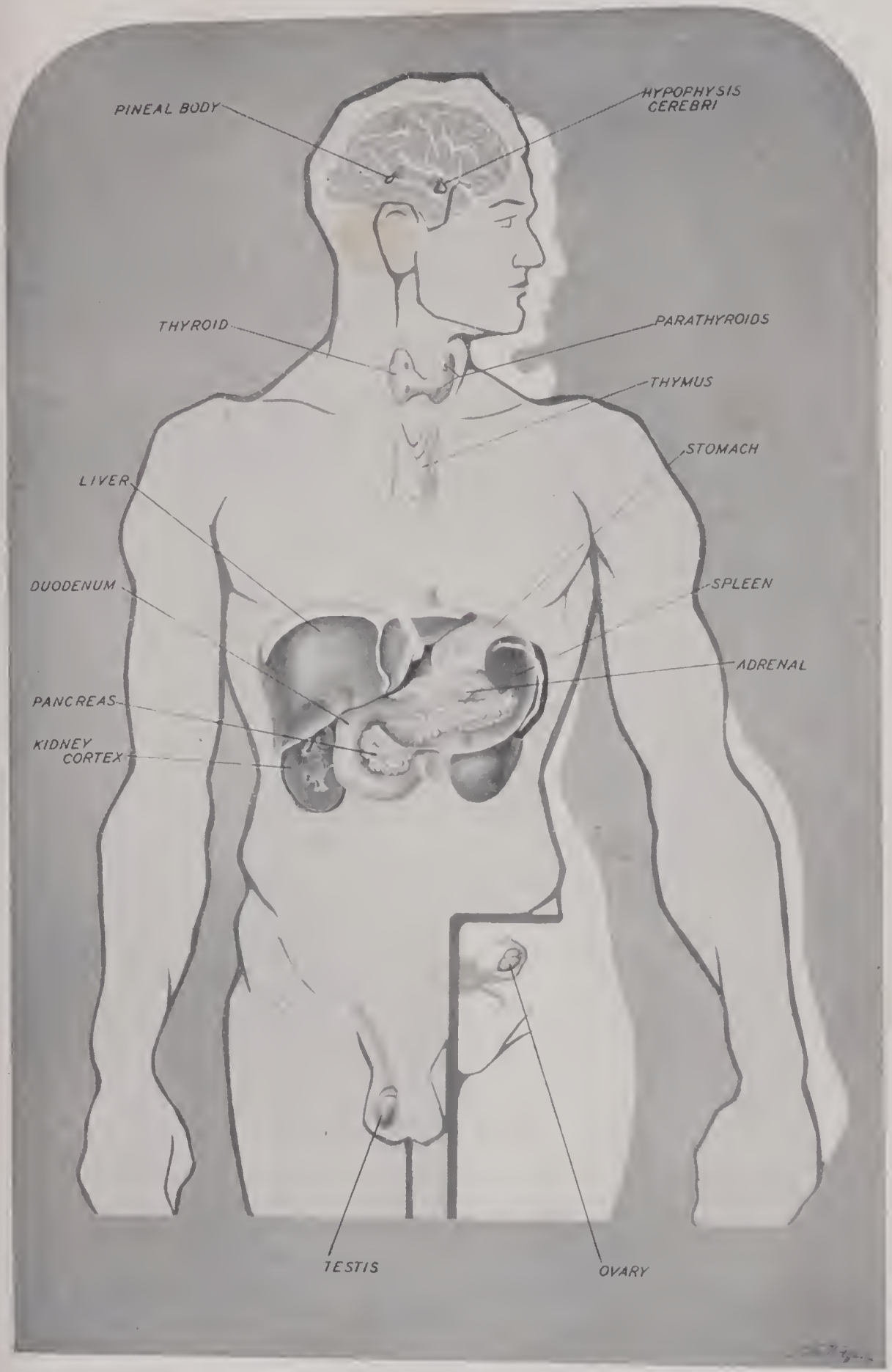


Fig. 140. The approximate locations of the endocrine glands in man. Although the pineal body, thymus, spleen and stomach are shown, they are not definitely known to secrete hormones. (Turner, C. D.: General Endocrinology.)

he used had any effect other than a psychological one, but his claims stimulated a great deal of research. Since then, experiments on the nature and function of hormones have shown that to a large extent what we are physically, mentally and emotionally depends upon the action of our endocrine glands. Figure 140 shows the location of the glands of the human body known to secrete hormones.

Because extremely small quantities of a hormone produce marked effects, only small amounts are secreted at any one time. This makes the isolation of a pure hormone difficult. In order to obtain a few milligrams of pure female sex hormone, an extract had to be made of over two tons of pig ovaries!

I. THE THYROID GLANDS

All vertebrates, from the lowest fish to man, have a pair of glands called the **thyroids,** located in the neck. In man the two glands are joined by a narrow isthmus of tissue which passes across the front of the trachea, immediately below the larynx. Embryologically, the thyroids develop as outgrowths of the floor of the pharynx, but by the time a human embryo is ¼ inch long, this connection has been lost, and the glands exist as independent structures. Examined microscopically, the thyroid is seen to consist of groups of cuboidal epithelial cells, arranged in hollow spheres, one cell thick. Each cavity of the spheres contains the secretion of the cells, thus acting as a storehouse.

The hormone secreted by the cells is a protein called **thyroglobulin.** All the amino acids except one may be split off from this substance, leaving an active chemical, called thyroxine, which has all the physiological properties of thyroglobulin. Thyroxine is a single amino acid containing, among other things, four atoms of iodine per molecule. It was synthesized artificially in 1927, and much of the material administered to patients today is synthetic thyroxine. If two of its four iodine atoms are removed, the activity of the substance is greatly decreased, and if all four iodine atoms are removed, activity is completely lost.

The fundamental effect of thyroxine is to speed up the rate of metabolism of all the body tissues. When an extra amount is given, the body uses more oxygen, produces more metabolic wastes, and gives off more heat than it normally does. When the supply of thyroxine is inadequate, the basal metabolic rate falls to as little as 600 to 900 Calories per day, or between 30 to 50 per cent of the normal amount. It is easy to see why thyroxine is essential for growth and development of the young animal.

Deficiency in the amount of thyroxine secreted in an adult results in a condition known as **myxedema,*** a disease characterized by a low metabolic rate which results in decreased heat production. The body temperature may drop to several degrees below normal, so that the patient constantly feels cold. In addition, the pulse is slow and the patient is physically and mentally lethargic. The appetite usually remains normal, however, and since the food consumed is not used up at the normal rate, there is a tendency towards obesity. The skin becomes

* Any deficiency of a gland secretion is indicated by the prefix "hypo," while an oversecretion is designated by the prefix "hyper." Hence myxedema is a type of hypothyroidism.

waxy and puffy, owing to the deposition of mucus fluid in the subcutaneous tissues, and usually the hair falls out (Fig. 141). Myxedema responds well to the administration of thyroxine or dried thyroid gland. Since thyroxine is not digested appreciably by the digestive juices, it can be given by mouth.

Myxedema is caused by an underactivity or degeneration of the thyroid gland itself. Another type of hypothyroidism results when the diet contains insufficient iodine to make up the thyroxine requirement. In such a case the gland itself tends to compensate for the insufficiency by increasing in size. The resulting enlargement, known as a simple goiter, may be a small swelling, barely detectable by touching the neck,

Fig. 141. Myxedema. *A*, Woman who had had myxedema within the previous seven years. Note the puffy features and coarse, dry hair. She was rather obese (had gained 40 pounds in the seven years) and moved slowly and clumsily. *B*, After six months of treatment with dried thyroid substance the patient had lost 23 pounds without dieting; her skin and hair were less dry. (Courtesy of Drs. H. Lisser and R. F. Escamilla.)

or a large, disfiguring mass, weighing several pounds (Fig. 142). The symptoms accompanying the goiter resemble those of myxedema, but are much milder. This type of goiter occurs in areas where the soil lacks iodine, or in regions remote from the sea where seafood (which is rich in iodine) is unobtainable. The incidence of this type of goiter has been greatly reduced by modern packing and shipping methods which permit the transport of seafood to all parts of the country, and by the addition of iodine (as potassium iodide) to table salt. The efficacy of this preventive measure was demonstrated in Detroit, where in seven years the incidence of goiter in school children was reduced from 36 to 2 per cent.

Hypothyroidism which is present from birth is known as **cretinism.**

Children suffering from the disease are dwarfs of low intelligence who never mature sexually (Fig. 143). If treatment is begun early, normal growth and mental development can be effected.

Any type of hypothyroidism may produce unfortunate alterations in personality, typically a state of depression and dissatisfaction with life. In extreme cases a real psychotic condition, indistinguishable from dementia praecox, may result.

Hyperthyroidism results either from the overactivity of a normal-sized gland or from an increase in the size of the gland itself. In both cases the basic metabolic rate increases to as much as twice the normal amount, producing symptoms exactly the opposite of those caused by a subnormal metabolic rate. The excessively rapid heat production causes the hyperthyroid to feel uncomfortably warm, and to perspire profusely.

Fig. 142. A simple goiter, caused by insufficient iodine in the diet. (Crile, G., Jr.: Practical Aspects of Thyroid Disease.)

Because the food he eats is used up quickly, he tends to lose weight even on a high caloric diet. High blood pressure, nervous tension and irritability, muscular weakness and tremors are symptomatic of the condition. But probably the most characteristic symptom is the protrusion of the eyeballs, called **exophthalmos,** which gives the patient a wild, staring expression (Fig. 144). The swelling of the gland as the result of hyperthyroidism is known as **exophthalmic goiter,** to distinguish it from the simple goiter caused by insufficient iodine. Identical symptoms can be caused by feeding thyroid substance or thyroxine to normal people.

Hyperthyroidism can be treated only by removing some of the thyroid gland, usually by surgery, although radium and X-rays, which kill the individual cells, have also been used with success. Recently the disease has been treated by administration of the drug thiouracil, which inhibits

the synthesis of thyroxine. Another method of treatment, still in the experimental stage, is the injection of radioactive iodine. Since the thyroid accumulates iodine, the rays given off by it are concentrated in the tissue of the gland and destroy the cells.

In those vertebrates which undergo a change from larval to adult form the thyroid hormone controls the alteration. In frogs, for example, the metamorphosis of the tadpole into an adult frog is regulated by the thyroid, and if the gland is removed surgically, the young tadpole never develops into an adult. But young tadpoles which are placed in pond-

Fig. 143. A cretin, aged 3½ years. Note the protruding tongue, bulging abdomen, wrinkled skin and deformed bones. (Courtesy of Dr. E. Perry McCullagh.)

water containing small amounts of thyroxine, undergo a precocious metamorphosis and develop into completely formed adult frogs, the size of a large fly.

II. THE PARATHYROID GLANDS

The parathyroid glands are masses of tissue, about the size of a small pea, which, in man, are attached to or imbedded in the substance of the thyroid gland. There are usually four parathyroids, two in the upper part and two in the lower part of the thyroid, but there may be fewer

or more than this number. Although the parathyroids are located on or within the thyroids, they have a completely independent function and a different microscopic appearance. The parathyroid cells are in a compact mass quite different from the hollow, spherical arrangement of cells in the thyroid. Like that gland, they originate embryologically from outgrowths of the pharynx and are evolutionary remnants of the gill pouches of fish.

The secretion of the parathyroids, known as **parathyrin,** is essential for life, and unless it is injected, an animal whose glands have been removed surgically will die in about a week. In some of the early operations on human goiter the parathyroids were removed along with the thyroid, and death invariably followed shortly after. At first it was

Fig. 144. A woman with exophthalmic goiter. Note the marked staring expression of the eyes. (Courtesy of Surgery, Gynecology and Obstetrics.)

believed that death was due to the removal of the thyroid, but it is now known that removal of the thyroid is not fatal.

When the parathyroids are removed, the animal suffers muscular tremors, cramps and convulsions in response to stimuli which, in a normal animal, produce no response or only a slight twitch. This condition, called **tetany,** is due to an increased irritability of muscles and nerves, caused by a decrease in the calcium content of the blood and tissue fluids. The calcium content of the blood of a parathyroidectomized animal falls to about half the normal amount. If a solution of a calcium salt is injected into a vein of an animal in tetanic convulsions, the convulsions cease within a minute, and further convulsions can be prevented by the repeated injection or feeding of calcium. The amount of phosphorus in the blood increases as the calcium decreases and is decreased

by the injection of parathyrin. The basic function, then, of the parathyroid hormone is to regulate the calcium and phosphorus content of the blood and tissue fluids, although how it operates is unknown. Apparently, part of its action involves regulating the rate of calcium absorption from the digestive tract, and its subsequent rate of excretion.

Parathyroid deficiency is rare in man, although occasionally the glands are removed accidentally during an operation on the thyroid, and sometimes they degenerate as the result of an infection. If the deficiency is mild, tetany occurs only during excessive strain, as in childbirth, and is treated, like the more severe condition, by giving parathyrin or calcium, or both.

Hyperfunction of the parathyroids is brought about by tumors or enlargements of the glands, and is characterized by a high blood calcium level. Since the calcium comes, at least partly, from the bones, hyperparathyroidism is characterized by soft bones which are easily bent and fractured. The muscles are less irritable than normally, and may become atrophied and painful. As the level of calcium in the blood increases, the mineral is deposited in abnormal places, such as the kidney. The disease can be treated by removing the excess parathyroid tissue surgically, or by destroying it with x-rays.

Parathyrin has not been isolated in a pure state, and its chemistry is unknown, although the active hormone is believed to be a protein. It is inactivated by the digestive juices, and so cannot be administered by mouth.

III. THE ISLET CELLS OF THE PANCREAS

In addition to the cells which secrete the digestive enzymes, the pancreas contains clusters or islets of cells which look and stain differently and have no associated ducts. The existence of these cells was recognized for a long time before their function was understood.

In 1886 two German investigators, Minkowski and von Mehring, were studying the role of the pancreas in digestion by removing the gland surgically from dogs and noting the digestive disturbances which occurred. The caretaker in charge of the animals noticed that their urine attracted swarms of flies to the cages. Upon analysis, large amounts of sugar were found in the urine, and the resemblance to diabetes was recognized. This disease had been known since the first century A.D., but its cause was unknown, and no treatment was effective. A short time before Minkowski and von Mehring performed their experiments, the cure for myxedema—the feeding of the thyroid gland—had been discovered, and it was hoped that a similar feeding of pancreas, or the injection of pancreatic extracts, would cure diabetes. After 1892, when the discoveries were published, many scientists tried to prepare effective extracts of pancreas, but none of the preparations was very good, and many were toxic. The difficulty was that the digestive enzymes of the pancreas destroyed the hormone before it could be extracted and purified. Finally, in 1922, two Canadians, Banting and Best, obtained an active substance by making extracts from pancreases of which the ducts had been tied for several weeks, so that the enzyme-producing cells had

degenerated. Since the islet cells develop before the enzyme-producing cells in embryonic animals, they were also able to obtain active extracts from that source. Since January, 1922, when the extracts were first used in the treatment of human diabetes, **insulin,** the name they gave to the substance extracted from the islet cells, has added years of life to millions of diabetics. Since the work of Banting and Best, methods have been worked out for extracting insulin from ordinary beef and hog pancreas, obtainable at the slaughterhouse. Today the amino acid content of this protein is almost completely known, and the substance has been crystallized in the laboratory.

Because insulin is a protein, it would be destroyed by the digestive juices, if taken orally, and so must be injected. Ordinary insulin must be taken several times a day to maintain the proper level in the blood, but recently, a slightly different material, **protamine zinc insulin,** has been developed, which is absorbed from the site of injection more slowly, and for most patients one injection a day is sufficient.

The primary function of insulin is to control the metabolism of glucose. It is necessary for the storage of glucose as glycogen in the liver, and for the oxidation of glucose to yield energy. In persons suffering from diabetes mellitus these functions are interfered with, and a host of other metabolic processes are affected secondarily. Typically, a great deal of urine is excreted, leaving the patient dehydrated and thirsty. A high concentration of sugar occurs in the blood and urine, and there is a steady loss of weight with increasing weakness, until at last the patient becomes comatose and dies. In spite of the excess glucose in the blood, the amount of glycogen in the liver decreases, because the tissues, unable to utilize glucose normally, are forced to use fats and proteins instead. The increased oxidation of fats causes an accumulation of incompletely oxidized fatty acids, known as **ketone bodies,** which are toxic. These substances are volatile and have a sweetish smell, which gives to the breath of diabetics its peculiar, characteristic odor. The amino acids from the proteins of the body are converted to glucose, and this also is excreted. If carbohydrates are eliminated from the diet, the patient still excretes glucose, which comes from this breakdown and transformation of proteins.

Diabetes is fatal because of the toxicity of the accumulated ketone bodies, and the continuous loss of weight. The injection of insulin alleviates all the diabetic symptoms: the patient is enabled to utilize carbohydrates normally, and the other symptoms disappear. The action of insulin persists for a short time only, however, which is the reason why repeated injections are necessary. Technically, insulin does not "cure" diabetes, since the pancreas does not begin secreting its hormone again, but continued injections of it prevent the appearance of the symptoms and enable the diabetic to lead a normal life. The fundamental reason why the pancreas stops secreting adequate amounts of insulin is not known, but there appears to be a hereditary basis for it.

If, in the treatment of diabetes, too much insulin is injected, the blood sugar level falls drastically and shock results. The nerve cells of the brain require a certain level of glucose for their normal functioning; if this level is not maintained, they become overirritable, and convulsions,

unconsciousness and death may follow. There are rare cases of enlarged pancreases due to tumors, which produce so much insulin that the patients suffer from recurring attacks of convulsions and unconsciousness. These can be relieved by eating candy, but the condition is cured only by the surgical removal of part of the pancreas.

IV. THE ADRENAL GLANDS

Over the upper end of each kidney lies one of a pair of small glands, the **adrenals.** The two glands together weigh less than half an ounce, but they are richly supplied with blood vessels. Actually, the adrenal is a combination of two entirely independent glands: a dark brown central core, the **medulla,** and a pale pink, outer coat, the **cortex.** The two parts have quite different embryonic origins and cellular structures, and secrete dissimilar hormones. It just happens that, in man and other mammals, the two glands lie together; in some of the lower vertebrates the cells corresponding to the medulla and cortex are anatomically separate.

1. The Adrenal Medulla. The cells of the central core of the adrenal gland are derived embryologically from the same source as the nervous system, and in structure resemble nerve cells. The secretion of the medulla, **epinephrine,** is similar in its effects to sympathin, secreted by the tips of certain nerve cells (p. 270). Epinephrine, also known as adrenin and adrenalin, is probably the simplest hormone chemically (its formula is $C_9H_{13}O_3N$), and is now made synthetically.

The physiological effects of an injection of epinephrine are marked and varied. The hormone causes a rise in blood pressure, an increase in the heart rate, an increase in the glucose content of the blood, a decrease in the glycogen content of the liver, and an increase in the rate of blood coagulation. In addition, the skin becomes pale, because of the contraction of the arteries serving them, the pupils dilate, and the muscles which erect the hairs contract, producing gooseflesh. All these effects can be produced by stimulating the sympathetic nervous system.

The adrenal medulla is not essential for life; it can be removed surgically without interfering in any way with the normal functioning of the body. Ordinarily, the gland secretes a small amount of epinephrine continuously, the rate being controlled by the nervous system. It is the only hormone whose secretion is affected by nervous stimulation.

Some investigators believe that epinephrine is secreted during emergencies to coordinate the activities of the various parts of the body for fighting or escaping. Indeed, the various effects of epinephrine would enable the animal to fight more effectively; but whether the medulla actually secretes enough of the hormone during an emergency to produce this result is still open to question. Adrenalin is widely used as a drug in treating asthma, in increasing blood pressure, and in starting the heart beat that has been stopped by electric shock.

2. The Adrenal Cortex. The adrenal cortex is a more complex gland than the medulla, both structurally, since it is made of three distinct layers, and functionally, since it secretes an unknown number of hormones.

When the adrenals are removed surgically from an experimental ani-

mal, the blood undergoes profound changes: the concentration of sodium and chloride decreases, the potassium concentration rises, and there is a loss of water resulting in a diminished blood volume, and hence a lowering of the blood pressure. Changes in carbohydrate metabolism also follow the removal of the cortex. The tissues apparently lose the ability to convert proteins into carbohydrates for oxidation. After a complete adrenalectomy, death ensues within a few days.

The human disease resulting from insufficient secretion of the adrenal cortex was first described in 1855 by the English physician Addison. **Addison's disease** is usually caused by a tubercular or syphilitic infection of the cortex which destroys its cells. It is characterized by low blood pressure, muscular weakness, digestive upsets, and a peculiar bronzing of the skin caused by the deposition of the pigment **melanin** (Fig. 145).

An oversecretion of the adrenal hormones sometimes results from tumors, which may appear at any age. In male children, overfunctioning of the cortex leads to precocious sexual maturity, with enlargement of the sex organs, and with the muscular development, hair distribution and voice of a mature man. Cortical overfunctioning in females causes masculinization—a beard, deep voice, regression of the ovaries, uterus and vagina, and growth of the clitoris so that it resembles a penis. These conditions can sometimes be corrected by the surgical removal of the adrenal tumor.

The cortical hormones are present in the cortex in small amounts only, and great quantities of cortical tissue must be extracted to obtain a few milligrams of the active substances. The first extracts to be successful in relieving adrenalectomized animals, and people suffering from Addison's disease, were made in 1927. At that time it was thought that perhaps a single hormone is secreted by the cortex, and the name **cortin** was given to the active material in the extract. Much research on the chemistry of cortin since then has shown that there are several cortical hormones. All those isolated so far belong to the class of chemicals known as steroids, to which the male and female sex hormones also belong.

From the foregoing we can conclude that the various cortical hormones perform three major functions in the body: they regulate the concentration of sodium, potassium and chloride in the blood and body tissues; they control the metabolism of carbohydrates, and especially the formation of carbohydrates from proteins; and they regulate the development of the sex organs, in a manner similar to that of the sex hormones.

V. THE PITUITARY

In a small depression on the floor of the skull, just below the hypothalamus of the brain, to which it is attached by a narrow stalk, lies a small gland about the size of a pea, the **pituitary**. This too is a double gland, of which one part, the anterior lobe, forms in the embryo as an outgrowth of the roof of the mouth, while the other (posterior) lobe grows down from the floor of the brain. When the two parts meet,

the anterior lobe grows partly around the posterior one, but the two lobes are distinguishable microscopically, even in the adult. The anterior lobe loses its connection with the mouth, but the posterior lobe retains its connection with the brain. The pituitary, like the adrenal, consists of two parts with quite different functions, which simply happen to be located together. In the whale the two parts are anatomically separate.

3. The Posterior Lobe. Two potent extracts have been prepared from the posterior lobe of the pituitary. One, known as **pitocin,** causes increased strength of contraction of the uterine muscles, and is sometimes

Fig. 145. A woman with Addison's disease. Note the bronzing of the skin which has occurred in patches. (Courtesy of Dr. George W. Thorn.)

injected during childbirth if the contractions are not sufficiently vigorous. Whether the posterior lobe normally secretes pitocin to aid in childbirth is unknown, but animals can give birth to their young quite easily after the posterior lobe has been removed. The other secretion, **pitressin,** causes a constriction of the small arteries of the body and thus a general increase in blood pressure. It is believed that the hormone secreted by the posterior lobe is a single protein substance having both these properties, but that in the process of being extracted and concentrated it is broken into smaller fragments, pitocin and pitressin, which are not proteins, but smaller molecules, resembling peptones.

Injury of the posterior lobe itself, or of the nerve tracts leading to it, may result in a hormonal deficiency causing **diabetes insipidus.** This disease, characterized by the failure of the kidney to concentrate urine, results in the patient's excreting as much as 10 gallons of urine daily, and hence suffering from excessive thirst. Injection of pitressin does not cure the disease, just as the injection of insulin does not cure diabetes mellitus, but it does relieve all the symptoms, and by repeated injections of pitressin the patient can live a normal life.

4. The Anterior Lobe. A number of different types of cells are distinguishable in the anterior lobe of the pituitary, each of which is believed to produce a different hormone. Six clearly defined fractions are known to be secreted, and there is evidence that half a dozen more may exist. All the fractions separated so far are proteins.

The importance of the pituitary in the body's economy is demonstrated by the symptoms which result when the gland is removed experimentally. Young animals whose pituitary is removed immediately stop growing and never reach sexual maturity. If adults are operated upon, both males and females show a regression of the reproductive organs, with the accompanying atrophy of both thyroid glands and the adrenal cortex. When pituitary extracts are injected into normal young animals, growth is stimulated and they become giants, reaching sexual maturity at an early age. The adrenal cortex, the thyroid and the sex organs respond by growing abnormally large and oversecreting.

The Growth Hormone. Giants have been known since the beginning of history, but it was not until 1860 that excessive growth was correlated with an enlargement of the pituitary. The first hormone from this gland to be discovered was the **growth-stimulating hormone,** finally isolated as a pure protein from extracts of beef pituitary in 1944. This hormone controls general body growth, and especially the growth of the long bones. Consequently, when the pituitary is overactive during the growth period, there is a general acceleration of the process, resulting in a very tall, though fairly well-proportioned person (Fig. 147). Most circus giants are of this type. If the pituitary is underactive during the growth period, a small, normally proportioned person, known as a **midget** (Fig. 146), is the result. Oversecretion of the growth hormone after normal growth has been completed, however, produces a condition known as **acromegaly.** Since by this time most of the parts of the body have lost their capacity for growth, only the hands, feet and bones of the face develop. The hands and feet become grossly enlarged, the jaws grow abnormally long and broad, and the bony ridges over the eyes, and the cheekbones enlarge, giving the acromegalic a heavy, unpleasant facial appearance (Fig. 148).

In 1930 a strain of hereditarily dwarf mice was discovered in which the dwarfness was due to the absence in the pituitary of the type of cells believed to secrete the growth hormone. When pituitaries from normal mice were grafted into the dwarf ones, they attained normal size.

The Gonadotropic Hormones. In addition to the growth hormone, the pituitary produces two different protein hormones which stimulate the primary sex organs of both sexes, the ovaries of the female and the

Fig. 146. *A*, Hypopituitary midget, 4 feet, 6 inches tall, aged 24 years. Most, if not all, of the pituitary hormones were being secreted in insufficient amounts. The patient showed hypothyroidism (due to lack of thyrotropic hormone) and sexual infantilism (due to lack of gonadotropic hormones). In the absence of suitable pituitary extracts, the patient was given testosterone and thyroxin. *B*, After four years of such treatment he had gained 6 inches in height. (Courtesy Dr. E. Perry McCullagh.)

Fig. 147. A hyperpituitary giant posed with two men of normal height. The giant, approximately 7 feet, 3 inches tall, had a large pituitary tumor, visible by x-ray. He also exhibits some of the characteristics of acromegaly—note the enlarged lower jaw and hands. (Courtesy of Dr. E. Perry McCullagh.)

testes of the male. Both are necessary for the achievement of sexual maturity and for maintenance of the sexual functions in mature animals. One of them, called **follicle-stimulating hormone,** or **FSH,** stimulates the development of graafian follicles in the ovaries, and the formation of sperm by the seminiferous tubules of the testes. The other, called **luteinizing hormone,** or **LH,** is necessary for the release of ripe eggs from the follicle and the formation of male sex hormone by the interstitial cells of the testes. The two hormones together regulate the menstrual cycle in women and the estrus cycles of other animals. If the pituitary

Fig. 148.—A case of acromegaly. The oversecretion of the growth hormone of the pituitary in the adult results in an overgrowth of those parts of the skeleton which are still able to respond. Note the enlargement of the lower jaw and hands and the thickening of the nose and ridges above the eyes. (Turner, C. D.: General Endocrinology.)

is removed during pregnancy, abortion invariably follows, indicating that some pituitary hormone, perhaps LH, but possibly another one, is essential for normal gestation.

The Lactogenic Hormone. The lactogenic hormone, now isolated in pure form, initiates the secretion of milk by the mammary glands if they have reached the proper condition of development under the stimulation of the sex hormones. If the pituitary is removed immediately after childbirth, the flow of milk from the mammary glands ceases. The lactogenic hormone is responsible also for much of the maternal instinct, and male animals injected with it develop an interest in the young, even of another species, making attempts to protect and care for them. If a male is treated first with female sex hormones and then with lactogenic hormone, his mammary glands can be made to secrete milk.

Other Pituitary Hormones. The pituitary controls most, if not all, of the other endocrine glands. An **adrenocorticotropic** hormone has been isolated which is necessary for the development and maintenance of the normal structure and functioning of the adrenal cortex, and a **thyrotropic** hormone is necessary for the development and functioning of the thyroid. Both the adrenal cortex and thyroid glands regress when the pituitary is removed, but this regression can be prevented or overcome by the injection of these hormones. The pituitary also secretes a hormone with effects opposite to those of insulin, called the **anti-insulin hormone,** and a **fat-metabolism** hormone, which, among other things, increases the content of fat in the liver. There is evidence, too, of the existence of a hormone which affects the parathyroid glands. Other, as yet undiscovered, hormones may be manufactured by the pituitary; it is difficult to separate particular ones because all of them are proteins which easily lose their efficacy in the process of being extracted and purified. Because of its prëeminent role, the pituitary has been called the master control of the endocrine system.

VI. THE TESTES

In addition to cells which manufacture sperm, the testes contain endocrine cells which produce the male sex hormone, **testosterone.** Those hormone-secreting cells, known as **interstitial cells,** are located between the seminiferous tubules which produce sperm (Fig. 149). Testosterone stimulates the development of the so-called secondary male sex characters—the beard, the growth and distribution of hair on the body, the deepened voice, the enlarged and stronger muscles, and the accessory sex structures, the prostate gland, seminal vesicles and penis. Castration, the removal of the testes, prevents this stimulation and results in a eunuch, a man with a high-pitched voice and beardless face. Since castration tends to make an animal larger, fatter and more placid, it has been practiced for centuries on domestic animals. The effects of castration can be reversed by the injection of testicular extracts or by the grafting on of testicular tissue. Testosterone, injected into a female, causes many of the secondary male sex characteristics to develop.

Testosterone belongs to a group of chemicals known as the steroids (its formula is $C_{19}H_{28}O_2$). The activity of this hormone is commonly measured by its ability to induce growth of the comb in a castrate chicken or capon. Pure testosterone is extremely potent: a pound of it would cause growth of the comb in 500,000 capons!

Evidence of the source of the male sex hormone came from a study of the condition in which the testes fail to descend into the scrotal sac, but remain within the abdominal cavity. When this happens, the man is completely sterile—unable to produce sperm—although he usually has normal secondary sex characteristics. When an undescended testis is examined microscopically, the cells of the sperm-forming tubules are found to have degenerated, but the interstitial cells lying between them are normal. For a long time it was not understood why the sperm-forming cells of the testis degenerated when the gland remained in the body cavity, since it received normal blood and nerve supply. Then it was discovered that the sperm-forming cells are particularly susceptible to

heat and require the approximately 3 degrees cooler temperature of the scrotal sac. The slightly higher temperature of the abdominal cavity destroys the sperm-forming cells, but not the interstitial, hormone-secreting cells. It is probable that an attack of fever temporarily sterilizes a man.

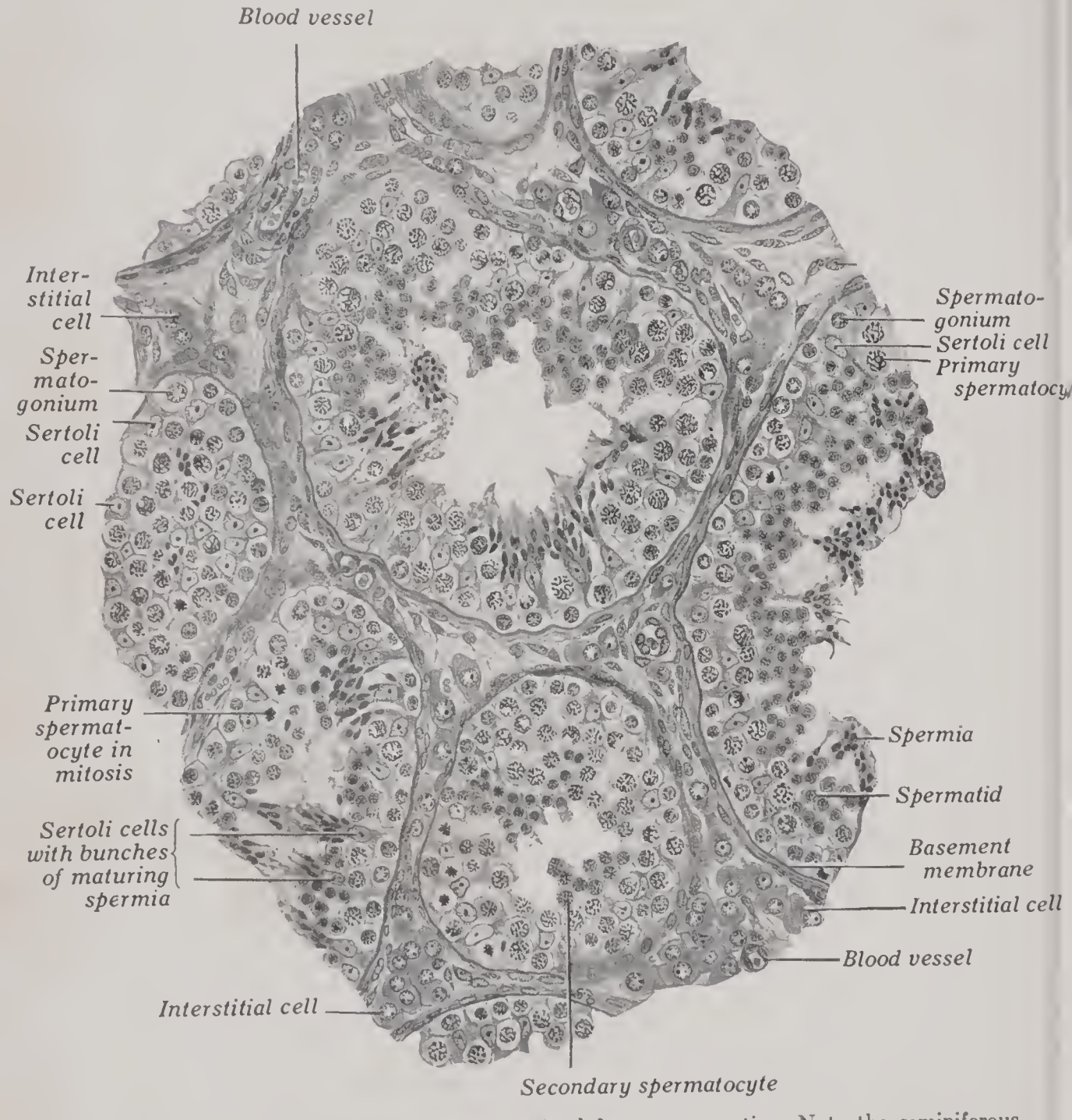


Fig. 149. Section of a human testis obtained from an operation. Note the seminiferous tubules seen in cross section, containing cells in various stages of spermatogenesis, and, between the tubules, the interstitial cells which secrete the male sex hormone. (Maximow and Bloom.)

The male sex hormone also determines sexual behavior to some extent, and is partly responsible for the sex urge. Many animals, even when castrated before reaching sexual maturity, will pursue females and exhibit mating behavior for months after castration, although eventually sexual behavior decreases.

Injection of testicular extracts and the grafting of testicular tissue into human males in the hope of obtaining a rejuvenating effect have been tried many times, but it is doubtful if anything more than a positive psychological effect has ever been obtained.

VII. THE OVARIES

Like the testes, the ovaries are endocrine glands, secreting sex hormones, although their primary function is usually considered to be the manufacturing of eggs for reproduction. The two ovaries are bean-shaped structures, about 1½ inches long, supported in the back part of the abdominal cavity by mesenteries. The outer layer of each gland is the **germinal epithelium,** from which the eggs develop, while the central part is composed of connective tissue and blood vessels. Just under the germinal epithelium is a thick layer of spherical groups of cells, or follicles, each enclosing an egg (Fig. 150). At birth, several hundred thousand of these have already originated from the germinal epithelium. Some degenerate, but the majority remain quiescent until the age of puberty, when the process of their growth and development begins.

Each month, one or more of the follicles begins to enlarge and becomes distended with follicular fluid, until it finally protrudes above the surface of the ovary and bursts, releasing the egg cell contained in it. This process is known as **ovulation.** The released egg passes by way of a channel called the **oviduct** to the **uterus.** If the egg meets and is fertilized by a sperm in the upper part of the oviduct, it eventually becomes imbedded in the uterine wall and begins to develop into an embryo. If no sperm are present, the egg degenerates.

Whether or not fertilization occurs, the follicular cells left after the rupturing of the follicle in ovulation multiply rapidly and fill the cavity left by the previous follicle. Because these cells are yellow, the structure is known as the **corpus luteum** (yellow body). About the size of a pea, it projects from the surface of the ovary and is visible to the naked eye. If fertilization does not occur, the corpus luteum lasts about two weeks, after which it degenerates and is absorbed. When fertilization occurs, the corpus luteum enlarges still further and remains throughout the period of pregnancy.

The primary female sex hormone, **estrogen,** is produced by the cells lining the cavity of each follicle. This substance is responsible for the body changes which occur in the female at the time of puberty or sexual maturity: the broadening of the pelvis, development of the breasts, growth of the uterus and vagina, growth of the pubic hair, change in the voice quality, and the onset of the menstrual cycle.

The second female sex hormone, **progesterone,** is produced by the cells of the corpus luteum. It is necessary for the completion of each menstrual cycle, because it completes the alterations in the uterus begun by the estrogen. It also makes possible implantation of the fertilized egg in the uterine wall, and causes development of the breasts during the latter months of pregnancy. Both female sex hormones are steroids, fundamentally similar to the male sex hormones and those of the adrenal cortex.

Both male and female sex hormones are produced by both sexes; in

fact, one of the richest sources of female sex hormone—one used commercially—is the urine of stallions. Recently, female sex hormones have been found in palm nut oil and pussy willows! What they are doing there no one knows.

5. The Estrus Cycle. In most mammalian species the females demonstrate rhythmic variations in the intensity of the sex urge. The period when it is at its height is known as **estrus,** and the animal is then said to be in heat. Cats and dogs have about two estrus periods each year, and most wild animals have only one, but some animals, such as the rat, have them as frequently as every five days. Most females of any species will accept the male in copulation only during the estrus period.

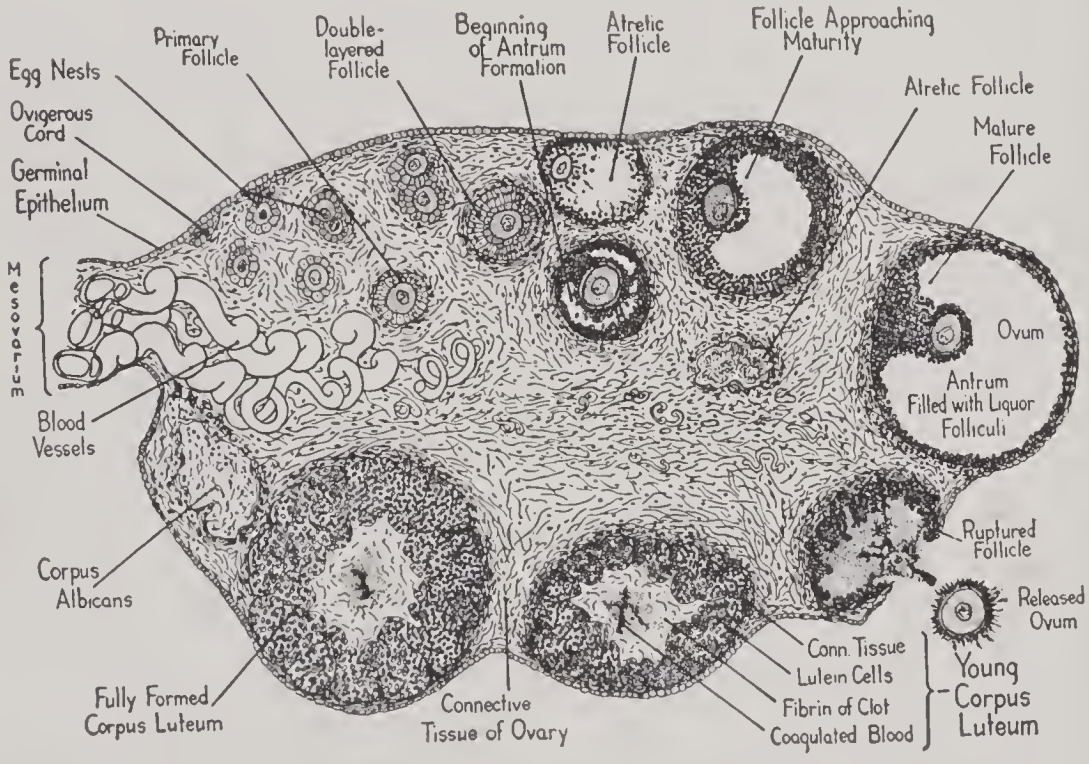


Fig. 150. Diagram of the stages in the development of an egg, follicle and corpus luteum in a mammalian ovary. Successive stages are arranged clockwise, beginning at the mesovarium (mesentery which holds the ovary in place). (Patten, B. M.: Human Embryology, The Blakiston Co.)

The estrus cycle is marked not only by the change in the intensity of the sex urge, but by changes in the lining of the vagina and uterus, which make the latter better able to receive a fertilized egg. The uterine lining becomes softer and thicker, while its blood vessels and glands increase in number and size. These processes reach their height a short time after ovulation, and if fertilization and the imbedding of a fertilized egg do not occur, the lining gradually reverts to its original condition.

6. The Menstrual Cycle. Human and anthropoid ape females do not experience any distinct period of estrus; instead, the cycle is marked by periods of bleeding, known as **menstruation,** which occur about every twenty-eight days and last about four days. The menstrual flow consists of pieces of the ruptured uterine lining, and blood from its vessels.

Since the lining of the uterus is almost completely destroyed by each

menstruation, it is thinnest just after the menstrual flow. At that time, under the influence of the follicle-stimulating hormone, or FSH, secreted by the pituitary, one or more of the follicles in the ovary begin to enlarge rapidly, while the follicular cells secrete estrogen. This hormone causes the uterine lining to grow, and by the end of the first week, it is about half as thick as it will become without pregnancy (Fig. 151).

Approximately fifteen days after the beginning of the previous menstrual period, ovulation occurs—the ripe egg is released from the ovary by the rupturing of the follicle. The follicular cells are then transformed into a corpus luteum, which, under the stimulation of the luteinizing

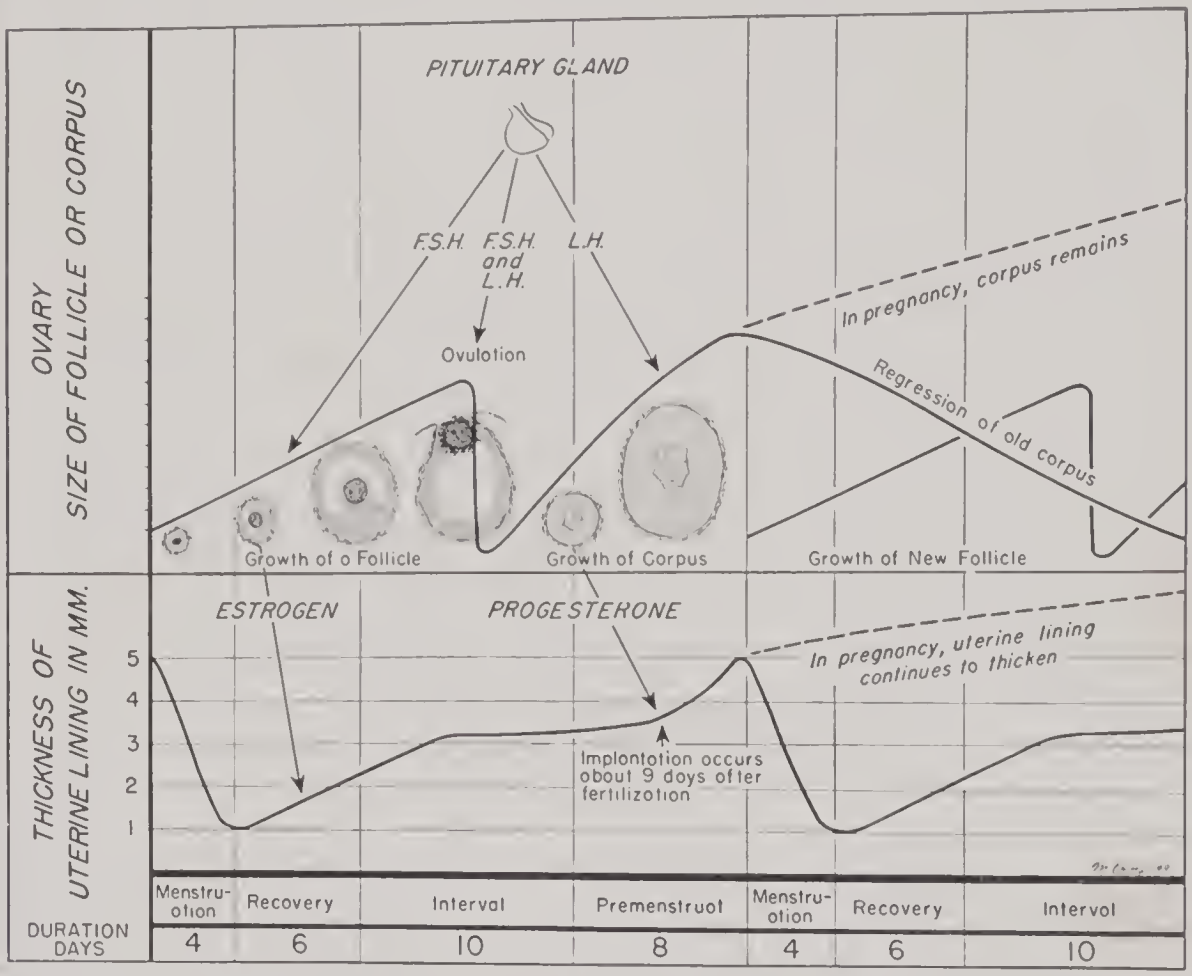


Fig. 151. The menstrual cycle in the human female. The solid lines indicate the course of events if the egg is not fertilized; the dotted lines indicate the course of events when pregnancy occurs. The actions of the hormones of the pituitary and ovary in regulating the cycle are indicated by arrows.

hormone, or LH, secreted by the pituitary, secretes the second hormone involved in the menstrual cycle, progesterone. This hormone completes the development of the uterine lining, preparing it to receive a fertilized egg. It also promotes the growth of the mammary glands, and prevents the development of any additional follicles and eggs.

If the egg has not been fertilized, about twenty-seven days after the beginning of the previous menstrual period the corpus luteum undergoes regression, thus terminating the secretion of progesterone. Since the uterine lining depends on the hormone for maintenance, this marks the beginning of its breakdown, and the menstrual flow begins. In the ovary, another follicle, released from the inhibition of progesterone, begins to ripen, and the next menstrual cycle starts.

If pregnancy occurs, the corpus luteum remains and secretes progesterone almost until the time of birth. The continued secretion of the hormone during the early months of pregnancy is necessary for its continuation, and if the corpus luteum is removed, pregnancy ceases at once with an abortion. The corpus luteum hormone also stimulates the growth of the mammary glands during the latter months of pregnancy and prepares them for the action of the lactogenic hormone of the pituitary, which is secreted shortly after birth and causes the flow of milk.

After the egg has been released from the ovary and is passing down the oviduct, it can be fertilized for a short time only, probably about twenty-four hours. When the sperm are deposited, through intercourse, in the female reproductive system, they quickly lose their ability to fertilize an egg, within forty-eight hours at the most. The period of maximum fertility in human beings, then, narrows down to the time of ovulation, about midway between successive menstrual periods.

The reason why women are subject to nervous upsets and fits of depression just before and during the menstrual period is now fairly well understood. The maintenance of emotional equanimity in women seems to depend on the presence of a certain amount of female sex hormone in the blood and tissues. But for a few days just before menstruation, when the corpus luteum has begun to regress and has stopped secreting progesterone, and the follicle for the next cycle has not yet begun to secrete estrogen, there is a measurable deficiency of sex hormone in the blood. Similar changes in disposition frequently occur at the menopause, a period beginning around the forty-fifth year, and lasting about two years, when the menstrual flow stops permanently, and the amount of sex hormones in the blood decreases. About a week before the onset of menstruation, the blood contains a maximum of hormones, and many women find they feel better and can work more efficiently then than at any other time.

VIII. THE PLACENTA

Although the placenta is primarily an organ for the support and nourishment of the developing embryo (see p. 355), it is also an endocrine gland, secreting a substance chemically similar to estrogen, which has the same effects. In addition, it secretes a substance similar to the luteinizing hormone of the pituitary. During pregnancy, large amounts of this hormone are produced, and the excess passes into the urine; this is the basis for several pregnancy tests. When small amounts of a woman's urine are injected into a female animal—a nonpregnant mouse, rabbit or rat—significant effects on the animal's ovaries are produced by the hormones in the urine if the woman is pregnant. The test is accurate and makes diagnosis of pregnancy possible as early as two weeks after conception, long before any other signs are apparent.

IX. OTHER ENDOCRINE GLANDS

Certain other organs of the body, although not usually considered endocrine glands, do produce hormones. These include the small intestine, which yields **secretin**, responsible for the flow of pancreatic juice, and the hormone **cholecystokinin**, which stimulates the contraction of

the gallbladder. The stomach, liver and kidney also are believed by some to have endocrine functions, but the evidence for this is not yet conclusive.

The **thymus,** a fairly large gland, existing only during childhood, lies at the upper part of the chest, covering the lower end of the trachea. Microscopically similar to lymph tissue, it produces one kind of white blood cells, lymphocytes. Since the gland is large in early life and regresses after puberty, attempts have been made to show that it secretes a hormone affecting sexual maturity, but clear evidence of this has not been obtained.

The **pineal gland,** a small, round structure on the upper surface of the thalamus, between the two halves of the cerebral cortex, has long been suspected of endocrine activity, largely because it has no other known function, but there is no evidence that it secretes a hormone. Neither its removal nor injection of extracts from it has any effect on experimental animals.

X. INTERRELATIONSHIPS BETWEEN THE ENDOCRINE GLANDS

For the sake of simplicity we have had to consider each gland and its effects separately. Recent research shows, however, that nearly every gland affects the functioning of almost every other one. We have already discussed the extensive control which the anterior pituitary exerts over the sex glands, the thyroid, the adrenal cortex, the pancreas, and probably others as well. Consider, for example how the pituitary affects the ovary, stimulating the production first of estrogen and then progesterone. These hormones, in turn, affect the secretion of hormones by the pituitary itself. Thus progesterone inhibits the pituitary from secreting FSH to start another menstrual cycle, until the previous one is completed or pregnancy terminates. Another example of interrelationship is the inhibitory effect in some species of the adrenal cortex hormone on the thyroid, so that when the former is removed, the thyroid becomes more active. Again, the control of sugar metabolism depends upon a complicated interrelationship between hormones of the anterior pituitary and adrenal cortex, as well as upon insulin. These are still being investigated.

XI. HORMONES IN LOWER ANIMALS AND PLANTS

Almost all animals have hormones, and growth hormones, called **auxins,** occur in many plants. Sex hormones, similar to the mammalian ones, are found in nearly all lower animals, including those primitive species of worms in which there are separate sexes. The moulting of insects and crabs, and the changes in color of fish, crabs and amphibia, are all under hormonal control. In the frog the color-controlling hormone is produced by the pituitary, and if the gland is removed, the animal becomes albino. The condition can be reversed by the injection of pituitary extract.

QUESTIONS

1. How is the endocrine system comparable to the nervous system? How does it differ from it?

2. Define a hormone. How would you go about proving that a particular gland secretes a particular hormone?

3. Where is the thyroid gland located, and what does it secrete?

4. Differentiate between myxedema, simple goiter and cretinism.

5. What is the result of hyperthyroidism?

6. What is the function of the parathyroid?

7. What is the importance of insulin in the body? Explain why the feeding of thyroid gland cures myxedema, while the feeding of pancreas does not cure diabetes.

8. What are the parts of the adrenal glands, and what functions does each part perform?

9. What is Addison's disease?

10. What are pitocin and pitressin, and what effects do they have on the body?

11. Why is the pituitary sometimes called the "master gland"?

12. What is the difference, causally, between a midget and an acromegalic?

13. What is ovulation, and when does it occur?

14. What is the function of progesterone?

15. Make a list of all the structures in the body known to be endocrine glands and the hormones secreted by each.

16. Discuss the ways in which a knowledge of physiology and psychology can help society to establish fair laws.

SUPPLEMENTARY READINGS

Hoskins, R. G.: *Endocrinology*. New York, W. W. Norton & Company, Inc., 1941.
A detailed but understandable discussion of clinical endocrinology.

Selye, H.: *Textbook of Endocrinology*. 2d ed. Montreal, University of Montreal Press, 1949.
An advanced discussion, profusely illustrated, of general and clinical endocrinology.

Turner, C. D.: *General Endocrinology*. Philadelphia, W. B. Saunders Company, 1948.
A clear, readable presentation of the biologic aspects of endocrinology.

PART IV

THE REPRODUCTIVE PROCESS

CHAPTER 19

METHODS OF REPRODUCTION

NEXT to the urge for self-preservation, the most fundamental instinct of organisms at every level of the animal kingdom is to preserve their speeies by reproduction. Every normal plant and animal has the physiologieal equipment with whieh to reproduee his kind, and even at the human level, motivations of personal well-being are rarely strong enough to interfere with the fulfillment of this biological obligation to the raee. Millions of species of plants and animals have become extinet, of eourse, but whatever the causes, it is almost certain that failure of the urge to propagate was not among them.

The proeess of reproduetion is not the same in all species of plants or animals. For some living things it eonsists of nothing more than the simple division of the organism to form two or more new organisms. No special organs or eells are necessary for the procreation of the new generation, and the individuals are not sexually differentiated. This type of reproduetion, ealled **asexual,** is the simplest and most primitive of the two possible types and probably was the only method for the earliest forms of life. At the present time many of the single-celled plants and animals, such as baeteria and amebas, still reproduce by asexual methods exelusively.*

How long this type continued to be the sole means of reproduction we do not know, but it is possible, by arranging certain plants in a series, to demonstrate how, in the evolutionary scale, the seeond kind of reproduetion may have come into existence. This more complex method, exhibited by most of the higher plants and animals, is called **sexual reproduction,** beeause it involves specialized cells, called **gametes** or **sex cells,** which are contributed by *two* individuals. The sex cells themselves are not alike: one type, called **eggs,** is produced by the female, and eontains a store of yolk for the developing organism (the embryo); another type, ealled **sperm,** is produced by the male, and eonsists of motile cells, which have lost most of their protoplasm and developed "tails" to aid them in swimming to meet the egg. In various ways the two are brought together, and combine to form the fertilized egg or **zygote,** whieh develops into the new individual. The biological advantage of the sexual system is that the best characteristics of two organisms can be reeombined genetically, thus giving rise to offspring better able to survive than either of the parents. Evolution by natural seleetion ean oeeur to any signifieant extent only where this recombination of traits takes place in eaeh generation.

But even the highest animals and plants may, under certain condi-

* Recent studies at Yale University indicate that some bacteria may reproduce sexually, though infrequently.

tions, reproduce asexually; the production of identical twins from the splitting of a single fertilized egg is a kind of asexual reproduction. And many organisms can reproduce either sexually or asexually—some, as we shall see, regularly alternate the sexual with the asexual method.

I. ASEXUAL REPRODUCTION

Living things can give rise to a new generation asexually in a number of ways. When the body of a parent simply splits into two more or less equal daughter parts, which become new animals, the process is called **fission.** This method occurs predominantly among the single-celled ani-

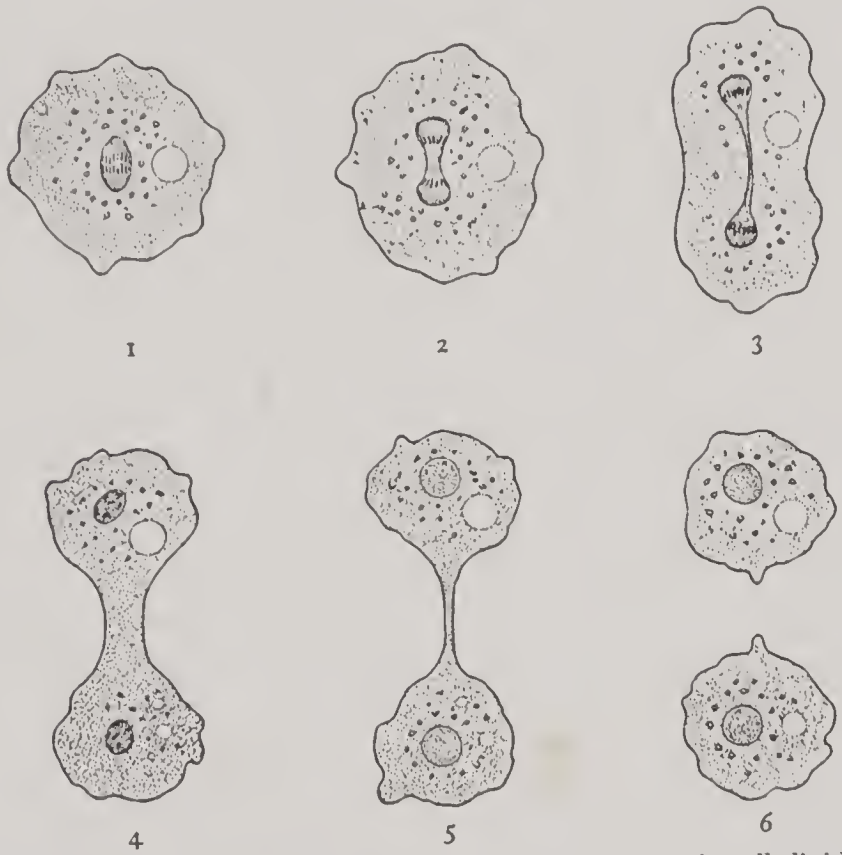


Fig. 152. Reproduction in an ameba, by simple fission. The single cell divides by mitosis. Note that the spindle and chromosomes lie within the persisting nuclear membrane. (Marsland and Plunkett: Principles of Modern Biology, Henry Holt and Co., Inc.)

mals and plants, such as amebas and paramecia (Fig. 152). The cellular division involved in the splitting takes place through mitosis (see p. 415).

Hydras and yeasts reproduce by another asexual method, called **budding,** which consists in the separation of a small part of the parent's body from the whole, and the development of this part into a new member of the species, which eventually takes up an independent existence.

Many higher animals—insects, starfish and lobsters—can grow a new leg, tail or other organ if one is lost. When this ability is carried to an extreme, it becomes a method of reproduction, called **fragmentation.** By this method the entire body of the parent may break into many pieces —in some species as many as several hundred—each of which develops into a new animal. The process is particularly common among flatworms, but starfish also have the ability to a high degree, and a single arm can regenerate a whole new starfish. At one time, when oystermen caught starfish feeding in oyster and mussel beds, they would cut them

in half and throw the pieees back into the water, believing they had killed them. But each half would quiekly regenerate, making twice as many predators for the oysters as before. Now oystermen know that starfish must be killed by being kept out of water.

Some animals and most plants reproduee asexually* by means of **spores,** which are special cells with resistant coverings, adapted to withstand unfavorable environmental conditions, such as excessive heat, cold or drought. When favorable eonditions occur, each spore develops into a new organism. Although plants are unable to move themselves, they can introduce their species into new locations by producing millions of these light spores which are carried by the wind. Some of the lower plants produee them simply by the division of any cell, but in higher plants they eome from special spore-produeing organs, called **sporangia.** The entire under side of a mushroom cap—that circle of fine, brown partitions—is the spore-produeing part.

Because the air is constantly filled with a variety of spores, things standing in a moist climate quickly develop mold plants, or become "moldy." Although reproduction by sporulation is especially eommon among plants—baeteria, fungi, mosses, ferns and seed plants—some animals, espeeially protozoa, do employ it.

One of the most interesting examples of reproduction by sporulation occurs in the single-eelled animal *Plasmodium,* which causes malaria fever. This organism has a complex life eyele involving both man and a certain mosquito, *Anopheles.* Through the bite of the mosquito, the malarial organisms infeet a person's blood stream, attacking the red blood cells, and eventually causing them to swell and disintegrate. Inside the red blood cell the Plasmodium divides into from twelve to twenty-four spores, each of which enters the blood stream when the eell disintegrates. Here, other red cells are infected and the process is repeated. The simultaneous breakdown of billions of red eells causes the malarial chill, followed by fever. If a second, uninfected mosquito bites the infected man, it becomes infected by sucking some of his blood. Inside the mosquito's stomach a complicated process of sexual reproduetion results in the formation of thousands of new spores, some of which get into the mosquito's salivary glands, ready to infeet the next man bitten.

There are many methods whereby higher plants reproduce naturally, or can be made to reproduce, by asexual means. Most of the cultivated trees and shrubs are reproduced from the cuttings of twigs, which sprout roots at their tips when placed in moist ground. This artifieial reproduetion is brought about to insure that the new plants will have the desirable qualities of the old ones. At the present time a number of commercial plants—bananas, seedless grapes, and navel oranges, to mention just a few—have lost the ability to produce funetional seeds and must be propagated entirely by asexual methods. When a farmer plants a potato, he is really doing the same thing, for a potato tuber is just a swollen stem of the potato plant.

Many plants, such as the strawberry, develop long horizontal stems called **runners.** These grow several feet along the ground, eventually to

* Among plants, the asexual method usually alternates with the sexual.

develop new roots at the tips and become new plants. Other plants spread by means of similar stems, called **rootstocks,** which grow underground. Such weeds as witch grass and crab grass are particularly difficult to control because they spread by means of runners or rootstocks.

II. SEXUAL REPRODUCTION

The most primitive type of sexual reproduction is found in the pond scum *Spirogyra,* which consists of long filaments of cells arranged end to end. In the fall, when reproduction usually occurs, any two cells from different filaments lying near each other many develop protrusions on their surfaces. These eventually grow into tubes which join to form a passageway from one cell to the other (Fig. 153), and the protoplasm

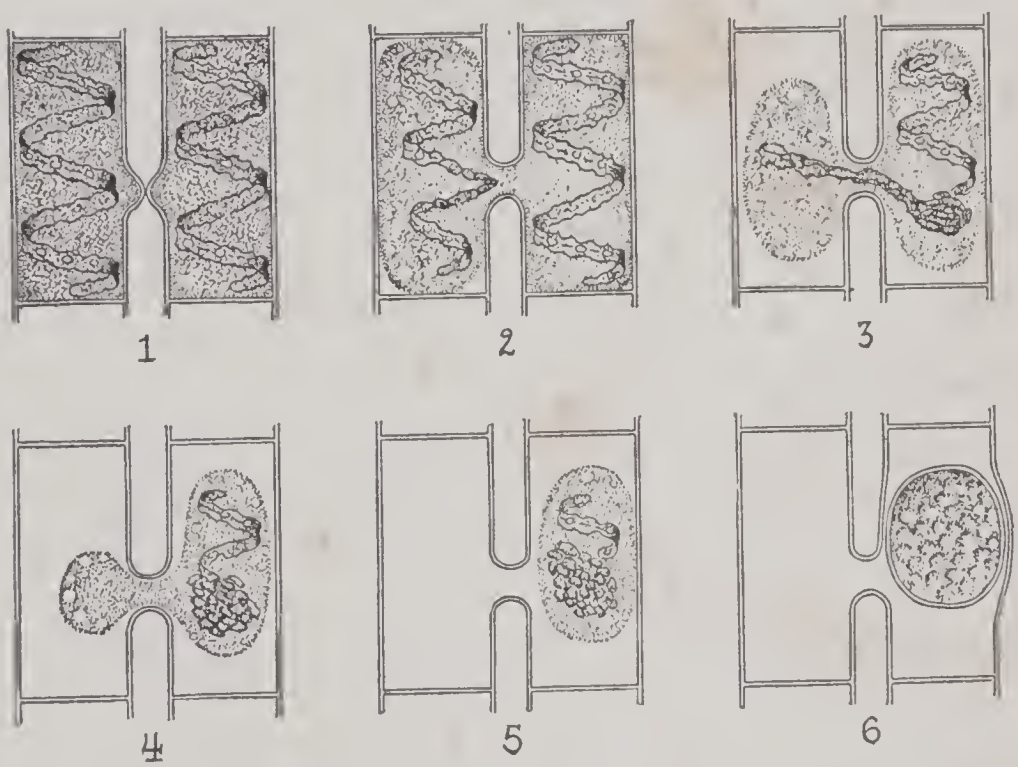


Fig. 153. Stages in the conjugation of two cells of the alga *Spirogyra.* A cytoplasmic bridge is formed between the two cells (*1* and *2*); the cytoplasm of one flows into the other (*3, 4, 5*) and unites with it (*6*). The nuclei of the two cells fuse to form a single one, and fertilization is thus achieved. (Marsland and Plunkett: Principles of Modern Biology, Henry Holt and Co., Inc.)

from one cell begins to ooze through the tube into the other cell, where it fuses with its protoplasm. Finally, the nuclei of both cells unite, and fertilization is complete. By developing a thick wall, the resulting cell, or zygote, is able to survive during the winter. In the spring it germinates, or breaks through its tough covering, and undergoes divisions to become the long filament of the summer form. Here, then, we have sexual reproduction by the fusion of two unspecialized, identical cells.*

Another filamentous green alga, *Ulothrix,* demonstrates the next step in the evolution of sex. In this plant an individual cell in the filamentous chain undergoes several divisions (Fig. 154) to produce a number of small cells, each with two flagella. These cells break out of the original cell wall and swim about until two of them meet and fuse. The resultant

* The terms "unspecialized" and "identical" are used relatively. Since sexual reproduction is involved, the cells are not identical *genetically.*

zygote, like that of *Spirogyra*, develops a thick wall to withstand cold or drying. It later undergoes division and germinates to form the filament. This illustrates sexual reproduction by the fusion of two specialized though identical cells.

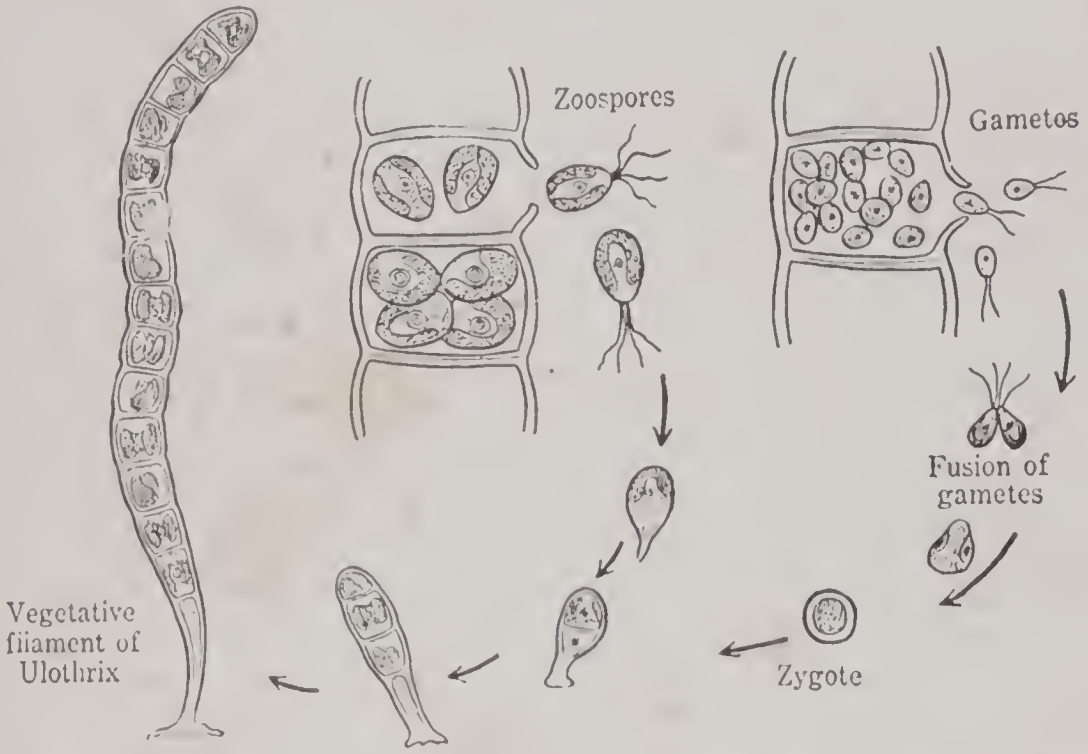


Fig. 154. Reproduction in the alga, *Ulothrix*. Both asexual reproduction, by means of zoospores, and sexual reproduction, by the fusion of gametes, are illustrated. (Young, Hylander and Stebbins: The Human Organism and the World of Life, Harper & Brothers.)

A third step in the evolution of sexual reproduction is demonstrated by yet another alga, *Oedogonium*, in which the cells which fuse to form

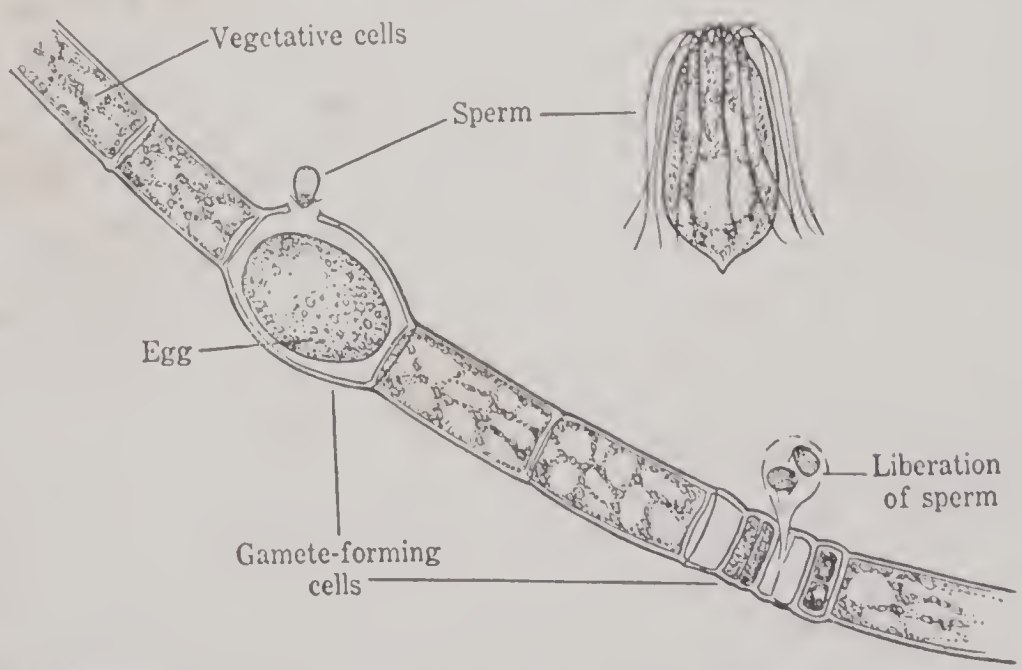


Fig. 155. Reproduction in the alga *Oedogonium*. In this alga the two types of gametes—eggs and sperm—can be clearly differentiated. (Young, Hylander and Stebbins: The Human Organism and the World of Life, Harper & Brothers.)

the zygote are unlike, and have become differentiated into a large, nonmotile, food-laden egg and a small, motile sperm (Fig. 155). Certain

cells of the long filament of this plant develop into large gametes, replete with stored food and incapable of moving. Other cells of the filament undergo division and produce a small, ciliated, motile sperm, which escapes from the enclosing cell wall, swims in the water and eventually enters the cell containing the egg and fuses with it. The resulting zygote later divides and forms a new plant made of many cells connected end to end in a long filament.

The final step in the evolution of sex is exhibited by other algae, as well as by higher animals and plants, whose specialized gametes are produced only by special cells in the body—the sex organs—rather than by any cell in the organism, as in the three previously described organisms. The existence of these plants, which can be arranged in a series of increasing complexity in regard to their method of sexual reproduction, suggests that sex actually did evolve through a series of such intermediate steps.

Some animals reproduce either sexually or asexually. For the one-celled animal, paramecium, sexual reproduction is a complicated process in which two individuals come together on their oral surfaces, fuse, and exchange nuclear material. The original nucleus of each divides several times before one of the resulting nuclei migrates across to the other animal and fuses with one of its nuclei. After that the animals separate, and there is further nuclear and cytoplasmic division, eventually resulting in four individuals. It was once thought that sexual reproduction is occasionally necessary to rejuvenate the strain, but Woodruff of Yale has maintained a strain since 1907 without sexual reproduction and with no loss of vitality. More recently, Sonneborn has shown that although paramecia are not differentiated into two sexes, there are definite mating groups, and that individuals of one group will mate only with those of the other. Heredity determines which mating group an individual belongs to.

Among primitive algae, such as *Spirogyra* and *Ulothrix*, asexual and sexual reproduction may occur in the same plant, depending on environmental conditions. In all the higher plants, seed plants, ferns, mosses and the higher algae there is a definite, regular alternation of a generation of plants reproducing sexually with a generation reproducing asexually by means of spores.

III. THE LIFE CYCLE

The life cycle of any species may be defined as the biological processes of development which occur between any given point in an organism's life span, and that same point in the life span of its offspring. For animals such as amebas, which reproduce by splitting, the cycle is simple. A small ameba grows and divides, giving rise to two new amebas, which repeat the process. The human life cycle of growth, maturity, mating, and birth of the young, though more complicated, is still comparatively simple. Some of the parasitic worms go through a complex series of three, four, or even more forms before the life cycle is completed by the reappearance of the original form.

Among plants the generation which reproduces sexually through gametes is known as the **gametophyte,** and the generation reproducing

asexually by spores is known as the **sporophyte.** The life cycle of higher plants consists in the production of gametes by the gametophyte generation, the union of these to form a zygote, which develops into a sporophyte plant, the production of spores by the sporophyte, and the development of the spores into gametophyte plants. In mosses, ferns and

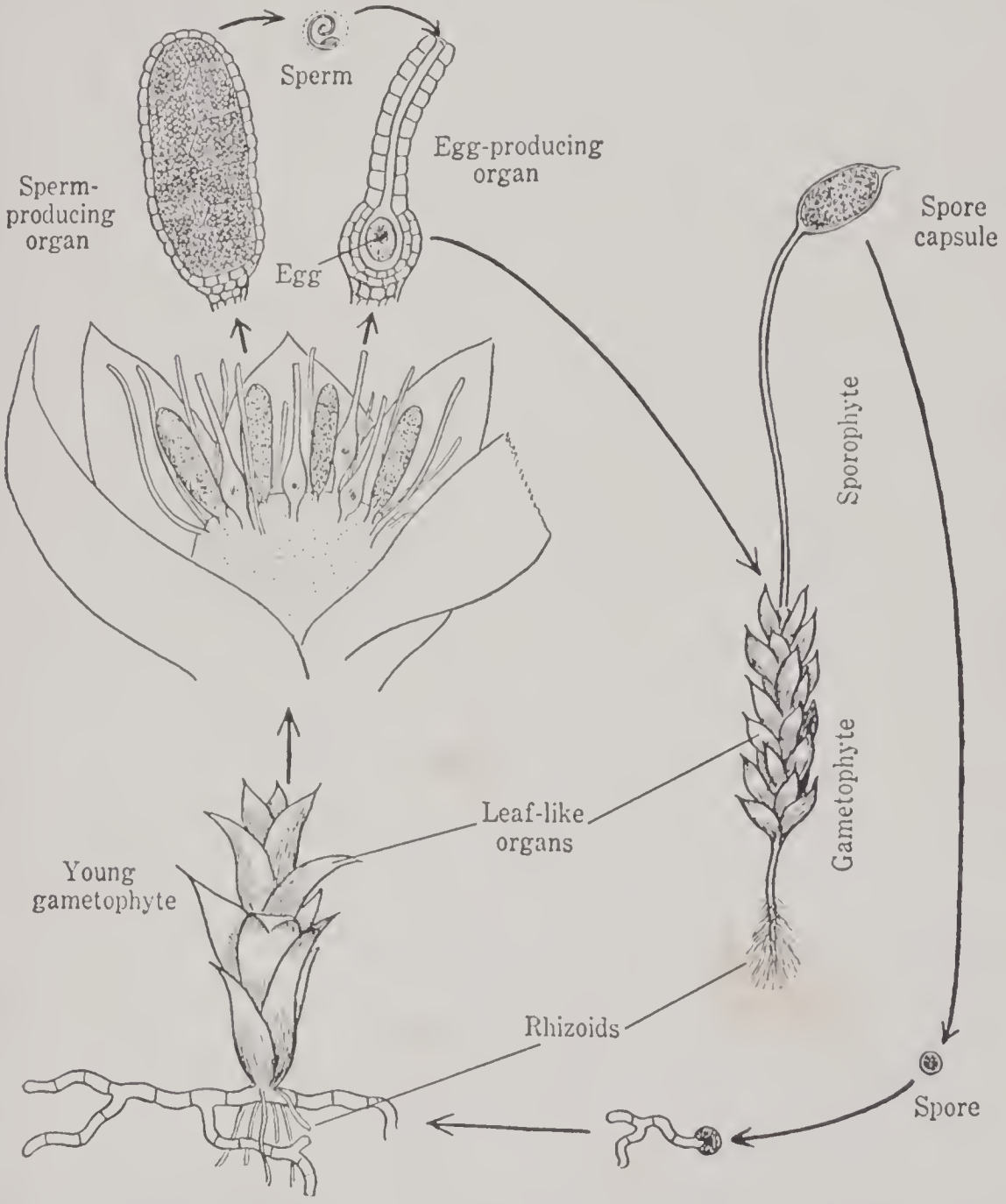


Fig. 156. The life cycle of a moss plant, illustrating the alternation of a generation (the gametophyte) which reproduces sexually, with a generation (the sporophyte) which reproduces asexually. (Young, Hylander and Stebbins: The Human Organism and the World of Life, Harper & Brothers.)

seed plants, relative size and duration of the gametophyte and sporophyte generations vary considerably.

1. The Life Cycle of Mosses. The familiar small, green leafy plants called moss are really the gametophyte generation of the whole plant. The gametophyte consists of a single central stem, surrounded by leaves and held in place in the ground by a number of slender rootlets, or rhizoids, which absorb water and salts from the soil. The leaf cells

produce, by photosynthesis, all the other compounds the plant needs for survival, so that each gametophyte is an independent organism.

When the gametophyte has attained full growth and is ready to reproduce, sex organs develop at the top of the stem, in the middle of a circle of leaves (Fig. 156). In some species the sexes are separate; in others, both male and female organs develop in the same plant. The male organs are sausage-shaped structures which provide a large number

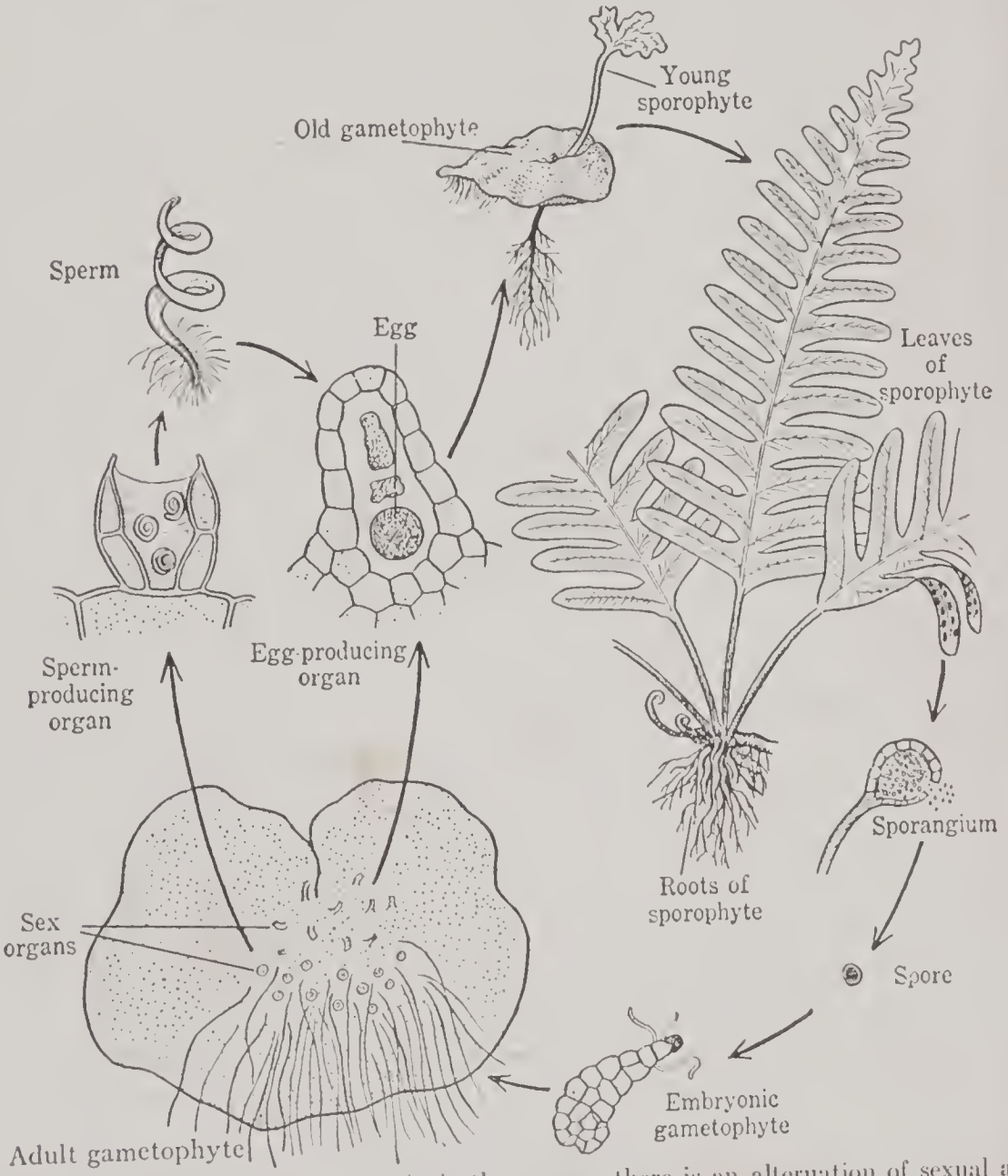


Fig. 157. The life cycle of a fern. As in the mosses, there is an alternation of sexual and asexual generations, but in the ferns it is the sporophyte generation which is the large, recognizable plant. (Young, Hylander and Stebbins: The Human Organism and the World of Life, Harper & Brothers.)

of ciliated sperm. After a heavy rain or dew the sperm are released and swim through the film of water covering the plant to a neighboring female sex organ, either in the same plant or another. The female organ, which is shaped like a flask, contains one large egg in its broad base. Directed by a chemical substance released by this organ, the sperm swim down its neck and into its base, where one sperm fertilizes the egg. The resultant zygote is the beginning of the sporophyte generation.

In contrast to the independent green gametophyte, the sporophyte is a leafless, brown, single stalk which lives as a parasite on the gametophyte, obtaining its nourishment by means of a "foot" which grows down into the gametophyte tissue. On the opposite, upper end of the sporophyte stalk, a capsule develops containing a number of spores, which are the beginning of the gametophyte generation. Eventually, these are released from the capsule and drop to the ground, where each develops into a gametophyte or, by budding, into several gametophytes, thus completing the life cycle of the plant.

2. The Life Cycle of the Fern. The life cycle of ferns involves an alternation of generations, each of which is an independent green plant. The relatively large, leafy plant commonly called a fern is the sporophyte generation; the gametophytes are tiny, free-living forms that exist only long enough to give rise to the new sporophytes.

The mature sporophyte consists of a number of leaves or fronds, each of which is subdivided into a large number of leaflets (Fig. 157) attached to the horizontal stem that lies just under the surface of the soil. From the stem a number of slender roots penetrate the soil. The under surfaces of the leaflets develop numerous small, brown sporecases, each with a large number of spores. The sporophyte plant may live several years and produce several yearly crops of them. At the proper time the spores are released, drop to the ground, and develop into flat, green, heart-shaped gametophytes, about the size of a dime. The gametophytes grow in moist, shady places, especially under decaying logs. From them, a number of roots grow into the soil to absorb water and salts. The male and female sex organs develop on the under surface of the gametophyte. Each female organ, usually lying near the notch of the heart-shaped structure, contains a single egg. The male sex organs, located at the other end of the gametophyte, develop a number of flagellated sperm, which are released after a rain and swim through the water on the under surface of the gametophyte to reach the eggs. When an egg has been fertilized, it develops into a new, large sporophyte to complete the cycle.

3. The Life Cycle of a Seed Plant. Such seemingly dissimilar plants as trees, shrubs, flowers and grasses are all alike in being seed plants, and are of a higher order than the ferns and mosses. The alternation of two generations—gametophyte and sporophyte—still takes place, but the gametophytes are reduced to a few cells lying within the tissues of the sporophyte flower. The sporophyte is the familiar, visible tree, shrub or grass. Not all flowers are easily recognizable as such: grasses and some trees have small green flowers which are quite different from the colorful blossoms we usually think of as flowers.*

The flowers of seed plants exist simply to assist in the reproduction of the plant, and consist of a number of leaves modified in one way or another for this purpose. In contrast to the method of spore production in ferns, where spores are produced on the underside of every leaf, only certain modified leaves in specific parts of the flower produce the spores of seed plants. A typical flower is made up of four concentric rings of parts (Fig. 158), although in any particular species some of the parts may be fused or missing. The outermost leaves, usually green and the

* Conifers and a few other seed plants do not have flowers.

most like ordinary leaves, are called **sepals**. Inside the ring of sepals are the **petals**, typically brilliant in color to attract insects and birds, thereby insuring pollination. Within the petals is a ring of **stamens**,

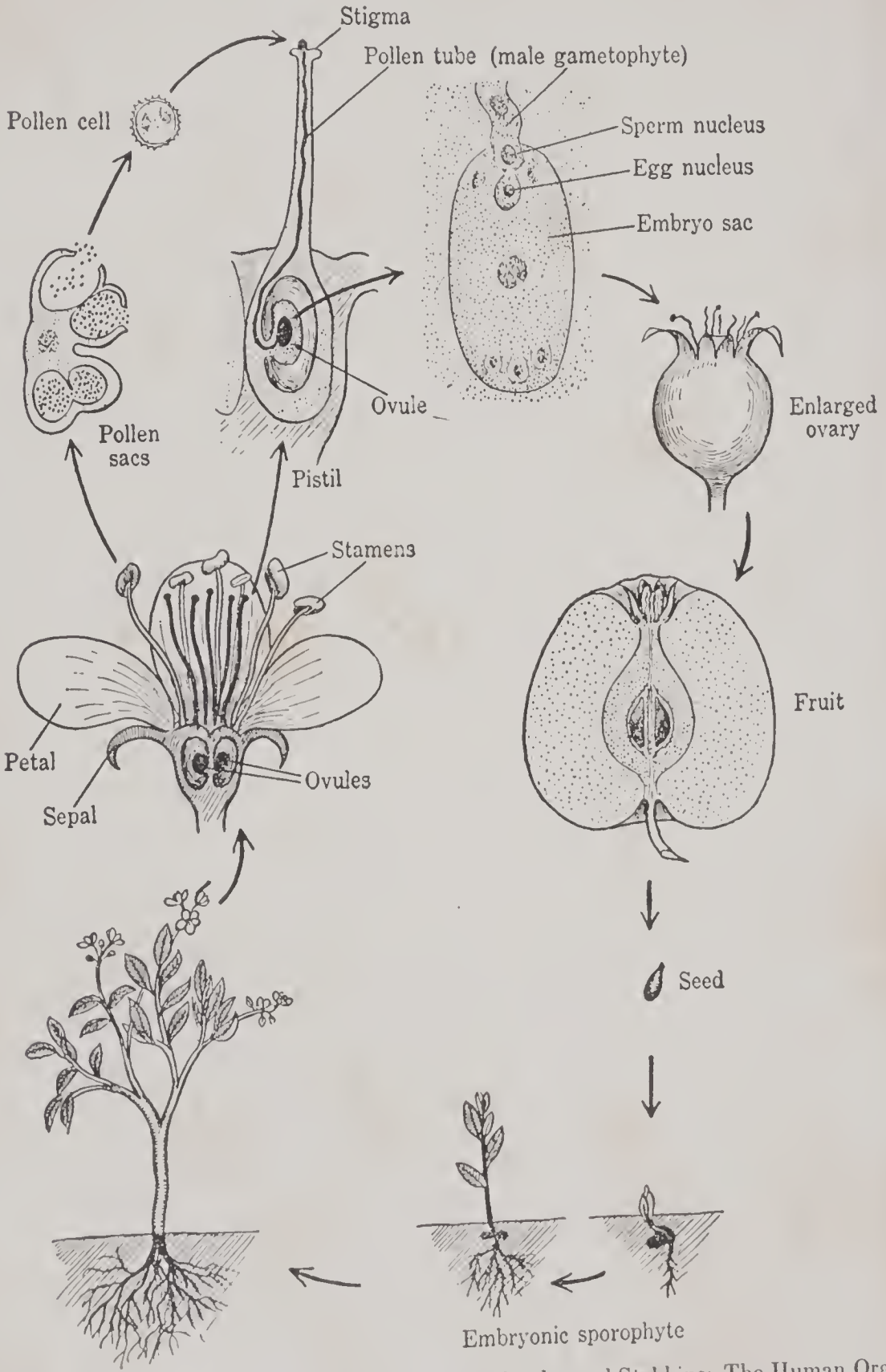


Fig. 158. The life cycle of a seed plant. (Young, Hylander and Stebbins: The Human Organism and the World of Life, Harper & Brothers.)

which produce the small spores in which male gametophytes and gametes develop, and in the very center of these is a ring of **pistils** (or a single, fused one) which yields the female gametophytes and gametes.

Variations in the thousands of kinds of flowers are due to differences in the number, arrangement, shape and color of these four basic parts. While still inside the stamen, the spores develop into tiny male gametophytes by nuclear division. The nucleus of the spore cell divides into two nuclei, one of which divides again, resulting in a total of three nuclei, without any division of the cytoplasm. This cell, with its three nuclei, is the equivalent of the male gametophyte of the lower plants, and is called a **pollen grain.**

Meanwhile, within the enlarged base of the pistils or ovary the bigger, female spores are developing. The ovary contains one or more ovules, each of which is a thick-walled structure bearing a single large spore. The spore germinates within the ovule, and the nucleus divides twice to form the female gametophyte. One of these four nuclei enlarges to become the egg nucleus—the female gamete; another becomes the **endosperm nucleus,** eventually the stored food of the seed.

Although most seed plants have flowers containing both male and female gametes, self-fertilization is comparatively rare. Usually, the pollen grains are transported by insects or the wind from one plant to another, permitting cross fertilization. When the pollen grain reaches the pistil, it is held in place by a sticky substance secreted by the latter and is stimulated to grow a long tube, the **pollen tube,** which extends down the pistil to the ovary. The male gamete—one of the three nuclei of the pollen grain—then passes down the pollen tube and fuses with the egg nucleus to form the zygote. A second nucleus of the pollen grain fertilizes the endosperm nucleus, giving rise to the tissues nourishing the embryo. As soon as the zygote has formed, it begins dividing to form the embryonic plant, while the fertilized endosperm nucleus divides to form a large mass of food-storing cells. The walls of the ovule, having grown and become thick, form the tough, outer covering of the **seed.** A seed, then, consists of the embryo plant, plus stored food in the form of endosperm, enclosed in a resistant covering derived from the wall of the ovule. While the seed is developing, the other parts of the flower usually wither and die, releasing the seed.

The embryo plant within the seed consists of a short stem, one or two leaves, and a small bud. Some seeds germinate immediately, others only after a winter has intervened. When the proper conditions of warmth and moisture are present, the seed bursts, and its enzymes digest the stored endosperm, making food available for growth. The stem elongates, sending a root downward and pushing the one or two leaves upward until they break through the surface of the soil. When this happens, the shoot begins to develop chlorophyll and to manufacture its own food by photosynthesis. The next sporophyte generation, which begins with fertilization of the egg nucleus by nucleus from the pollen tube, is now well on its way to maturity.

This method of reproduction, involving seeds, facilitates the spreading of the plant from one location to another. Some seeds have feathery plumes, enabling them to float great distances. Others have hooks with which to become attached to the fur of animals and so be carried far from their point of origin. A third device for seed dispersal consists in the development of fleshy fruits around the seed. When a fruit such as

a berry, apple or cherry is eaten and digested by some animal, the outer covering, being resistant to the digestive juices, passes through the digestive tract and allows the seed to be eliminated unharmed and develop normally, often at some distant point.

In the strict botanical sense, a fruit is a matured ovary containing seeds—the matured ovules. Therefore, although we usually think of only such sweet, pulpy things as grapes, berries, apples, peaches and cherries as fruits, bean and pea pods, corn kernels, tomatoes, cucumbers and watermelons are also fruits.

There are two main types of fruit: **true fruits,** consisting solely of the ovary tissues, and **accessory fruits,** containing parts of the sepal or stem in addition to the ovary. The edible fleshy strawberry, as a whole, is an accessory fruit which is really the enlarged tip of a stem. The yellow "seeds" are the individual true fruit. Apples and pears are other examples of accessory fruit. The true fruit of the apple is the core, and the edible part is derived from the stem and sepals of the apple blossom.

Some plants have true fruits which are fleshy; others have ones which are hard and dry. Grapes, tomatoes, bananas, oranges and watermelons are examples of fleshy fruit in which the entire wall of the ovary becomes pulpy. Peaches, plums and olives are examples of fruit in which only the outer part of the ovary wall becomes soft and fleshy, the inner part hardening to form the pit or "stone," containing the seeds. Nuts are examples of fruit in which the ovary tissue becomes hard and dry. There are, then, many kinds of fruit, differing in the number of ovules per fruit and the number of seeds per ovule, as well as in color, shape, water and sugar content, and consistency.

IV. SEXUAL REPRODUCTION IN ANIMALS

A few animals—primarily certain coelenterates—give rise alternately to a sexual and an asexual generation, in a manner similar to that of plants. But most animals not only reproduce solely by sexual means, but have permanent sexual organs.

4. Hermaphroditism. Many of the lower animals have both testes and ovaries and so produce both sperm and eggs, a condition known as **hermaphroditism.** Of this group, most of the parasitic flatworms, such as the tapeworm, are capable of self-fertilization. Since a host may be infected with a single parasite only, this ability is an important factor in the survival of the species. Most hermaphrodites, however, do not reproduce by self-fertilization; rather, two animals come together in copulation, each inseminating the other. This method is used by earthworms. In other species, self-fertilization is prevented by a development of the testes and ovaries at different times. Oysters, for example, are first male, then female.

5. Parthenogenesis. A rather rare modification of sexual reproduction, common among honeybees, wasps and certain other arthropods, is **parthenogenesis,** the development of an unfertilized egg into an adult animal. Some species of arthropods consist entirely of females which reproduce in this way. More commonly, parthenogenesis occurs for several generations only, after which males develop and fertilize a generation of eggs. Often, fertilization occurs in the fall, and the fertilized eggs are

quiescent during the winter. Among honeybees the female or queen bee is fertilized by a male just once in her entire life time. The sperm she receives is stored in a little pouch connected with her genital tract, and closed off by a muscular valve. As the queen lays eggs, she can either open this valve, permitting the sperm to escape and fertilize them, or keep the valve closed, so that the eggs develop without fertilization. The fertilized eggs become females—queens and workers; the unfertilized eggs become males (drones). Some species of wasps give birth alternately to a parthenogenetic generation and one from fertilized eggs.

Eggs from species which do not normally undergo parthenogenetic development can often be stimulated artificially to develop without fertilization. Frog eggs can be so stimulated by pricking them with a fine needle, and others can be made to divide by shaking them, adding chemicals to the water in which they are lying or, as in marine eggs, by changing the concentration of salt in the water. The animals resulting from artificial parthenogenesis are often weaker and smaller than normal, and may be unable to complete development. But adult frogs and rabbits have been produced by this means in the laboratory of Dr. Pincus of Clark University.

Many species of worms, and most of the other animals farther along the evolutionary scale, have permanent structures for sexual reproduction. Among the vertebrates a wide assortment of accessory structures has evolved to facilitate the union of egg and sperm, and to ensure the development of the embryo.

6. Types of Fertilization. Most aquatic animals simply liberate their sperm and eggs into the water, so that their union is haphazard. No accessory structures are needed, except the ducts which transport the cells to the outside of their bodies. This, the most rudimentary and uncertain method of uniting the gametes, is called, for obvious reasons, **external fertilization.**

Other animals, especially those living on land, have accessory sex organs for transferring the sperm from the body of the male to that of the female, so that fertilization occurs within the latter. This method, called **internal fertilization,** requires the cooperation of the sexes, and many species have evolved elaborate patterns of mating behavior to insure that it takes place.

An unusual one is that exhibited by the salamander: the male clasps the female and rubs her nose with his chin; he then dismounts in front of her, and deposits on the ground a spermatophore, a sac containing a large number of sperm. The female picks up the sac and places it in her cloaca. Here the sac breaks, releasing the sperm to fertilize her eggs.

Many breeding habits are dangerous or even fatal to the animals performing them; for instance, salmon swim hundreds of miles upstream to spawn and die; and the male spider is frequently eaten by the female after he has performed the necessary act of inseminating her. Yet, as we noted earlier in the chapter, the survival of the species requires that the individual sacrifice his own interests in the performance of these acts.

The evolution of instincts for the care of the young has accompanied the evolution of more efficient methods for bringing about fertilization.

Fish and amphibia in general take no care of the developing eggs, and great quantities must be laid each year in order that by chance a few will develop. The eggs of reptiles are usually laid in the sand or mud, where they develop without parental care, warmed only by the sun. Birds lay their eggs in nests, and incubate them by sitting on them. The newly hatched birds are quite helpless and require parental attention for several weeks.

In contrast to these eggs which develop more or less at the mercy of the environment, the mammalian egg (with the exception of those of the monotremes, which are laid and develop outside the body) develops within the uterus of the female, where it is safe from predators and from environmental changes until it is able to cope with them.

The young of many vertebrates—primarily the amphibians—do not resemble their parents at all, but go through an early larval form. At the proper time the larva, such as a tadpole, undergoes a relatively rapid change, or **metamorphosis,** to become the adult form. In general, the existence of the larval form is correlated with a relatively small amount of yolk in the egg, so that the young must become self-supporting at an early time. The larvae of many insects are specially adapted to feed and store food, while the adult animal eats nothing and lives only long enough to reproduce.

In the evolution of the vertebrates from fish to man, the trend has been towards the production of fewer eggs, and the development of instincts for parental care of the young. Thus the codfish produces millions of eggs a year, few of which ever develop into adult fish, while mammals, such as man, have few offspring, but take such good care of them that the majority reach adulthood.

QUESTIONS

1. Differentiate between sexual and asexual reproduction.
2. What are spores?
3. Are specialized sex organs necessary for sexual reproduction?
4. Trace the evolution of sex in plants as exemplified by living plants.
5. Differentiate between the gametophyte and the sporophyte generations.
6. What is a life cycle?
7. How do seed plants differ from other plants?
8. Name the parts of a flower and state the functions of each part.
9. Define the following: hermaphroditism; parthenogenesis.
10. Compare the devices used by different vertebrates to ensure fertilization.
11. Are human beings capable of regeneration? If so, to what extent?
12. Give an example of how, in human society, social pressure operates to insure the continuance of the species.

SUPPLEMENTARY READINGS

Hunter, G. W., and Hunter, F. R.: *College Zoology.* Philadelphia, W. B. Saunders Company, 1949.
A discussion of reproduction in invertebrates and vertebrates.

Pycraft, W. P.: *The Courtship of Animals.* 2d ed. London, Hutchinson and Co., 1933.
An interesting account of mating instincts in animals.

Young, C. W., Stebbins, G. L., and Hylander, C. J.: *The Human Organism and the World of Life.* New York, Harper & Brothers, 1938.
An interesting, elementary discussion of life cycles in plants.

CHAPTER 20

HUMAN REPRODUCTION

THE REPRODUCTIVE process in man represents a high expression of the evolutionary trends, observable in all the vertebrates, towards the production of fewer offspring and more assiduous parental care. Only a relatively few children are brought into existence during the lifetime of human parents, but these are well protected and cared for, not only during the actual period of development within the mother's body, but for years after birth.

In the vertebrates a number of accessory structures have developed to facilitate the transfer of sperm from the male to the female reproductive tract, and to provide a place for the development of the fertilized egg. These structures have evolved either from or in close association with the urinary system, and the two systems together are frequently referred to as the **urogenital system.**

Human reproduction, in common with that of most animals and plants, is accomplished sexually, by the union of specialized cells called gametes—ova or eggs produced by the female, and sperm produced by the male. All the parts of the complicated reproductive system in both sexes, as well as the various physiological and psychological phenomena associated with sex, have just one purpose: to insure the successful union of the egg and sperm, and the subsequent development of the fertilized egg into a new individual.

1. The Male Reproductive Organs. The testis, which so far we have discussed only as an endocrine gland, performs an equally important function as the source of the male sex cells. A pair of these glands develops within the abdominal cavity of all vertebrates, but in man, and some other mammals, they descend shortly before or after birth into the **scrotal sac,** a loose pouch of skin which is an outpocketing of the body wall. The cavity within the scrotal sac is part of the abdominal cavity, and during development is connected to it by a passageway, the **inguinal canal.** After the testes have descended through it, this canal is usually closed by the growth of connective tissue, so that the abdominal and scrotal cavities are separate. Occasionally, the inguinal canal reopens or fails to close, resulting in an inguinal hernia. In such cases a loop of the intestine may slip down into the scrotal sac and be caught there by the contraction of the abdominal muscles, which cuts off its blood supply. Unless an operation is quickly performed, the tissue of that part of the intestine dies. The normal descent of the testes into the scrotal sac is necessary for the production of sperm. If the testes remain in the abdominal cavity, as occasionally they do, the slightly higher temperature there prevents the formation of sperm.

Each testis consists of about one thousand highly coiled **seminiferous**

tubules, which actually produce the sperm, and, lying between them, masses of interstitial cells which produce the male sex hormones. The seminiferous tubules are lined with a germinal epithelium made up of rounded cells with large nuclei. These cells undergo division to form cells which develop into the sperm, with compact heads, containing the nucleus, and a long, whiplike tail for locomotion. In addition, the seminiferous tubules contain "nurse" cells which nourish the sperm as they develop from rounded cells into the mature, tailed form. The formation of sperm proceeds in waves along the tubules, so that the sperm which are not yet motile are moved along largely by the pressure of other sperm behind them.

At one end of each seminiferous tubule is a fine tube called the **vas efferens,** which connects it to a single, complexly coiled tube, the **epididymis,** where the sperm are stored. Each of the two epididymides lies close to the base of the testis to which it is attached. From each epididymis a duct, the **vas deferens,** passes from the scrotum through the remains of the inguinal canal, into the abdominal cavity, and over the urinary bladder to the lower part of the abdominal cavity, where it joins the urethra (Fig. 159).

As soon as the sperm are produced they are suspended in a liquid, the **seminal fluid,** which protects them as they are transferred to the female reproductive tract. This fluid is produced by three different glands. A short distance before the vas deferens joins the urethra, a pair of glands called the **seminal vesicles** empty into it by ducts. Farther on, around the urethra, at its source from the urinary bladder, are the **prostate glands** (in man these are fused into a single gland), which secrete their part of the seminal fluid into the urethra by two sets of fine, short ducts. Finally, farther along the urethra, at the base of the spongy tissue of the penis, lies a third pair of small glands, called **Cowper's glands,** which contribute the last component to the seminal fluid. This fluid has a complex composition and contains inorganic salts to act as buffers (sperm are sensitive to acids, and without these salts the acids normally present in the urethra and the female reproductive tract would kill the sperm before they could fertilize the egg), glucose for the metabolism of the sperm, and substances which lubricate the passages through which the sperm travel.

The **urethra** is a tube leading from the urinary bladder to the outside of the body. In the male the last part of it runs through the **penis,** the external reproductive organ, just above and in front of the scrotal sac. Within the penis the urethra is flanked by three columns of erectile tissue, which is spongy and thus capable of being filled with blood. Ordinarily, the spaces of the spongy tissue, though containing blood, are not distended, but during sexual excitement the arteries leading to these blood spaces dilate, while the veins draining them constrict, so that the spaces are filled with blood under pressure. This causes the penis to change from its usual flaccid state to become hard and erect, and thus able to enter the vagina. Ejaculation of the **semen**—the sperm in their seminal fluid—occurs when the penis is further stimulated by friction against the walls of the vagina, and is due to reflex waves of contraction

of the muscles of the vas deferens, the urethra and the associated glands.

2. The Female Reproductive Organs. The egg-producing organs of the female—the **ovaries**—are held in place by ligaments within the lower part of the abdominal cavity, between the hips. Each of the pair is about the size and shape of a shelled almond. When a girl reaches puberty there are some 30,000 eggs in each of her ovaries. Although there is some question about it, the latest evidence indicates that no new ones are ever produced thereafter. Since normally a woman ovulates

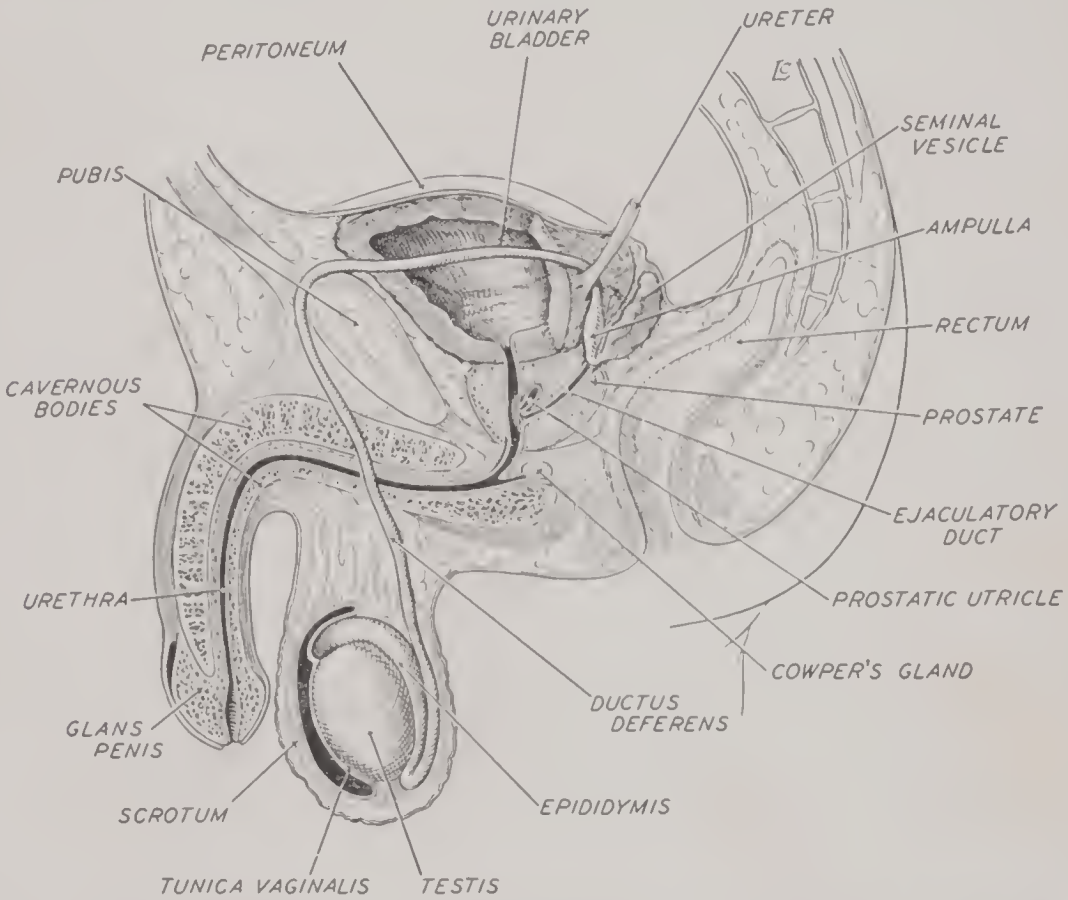


Fig. 159. Schematic sagittal section of the male pelvic region, showing the genital organs and their relations to the urinary bladder and urethra. (Turner, C. D.: General Endocrinology.)

thirteen times a year for approximately thirty years, and but a single egg ripens each month,* only 400 or so of these eggs ever reach maturity and escape from the ovary; the rest degenerate and are absorbed.

In contrast to the male reproductive tract, the female tract does not consist of a series of connected ducts. Instead, the egg is released into the abdominal cavity at the time of ovulation (p. 327), whence it passes into one of two tubes, called the **oviducts** or **fallopian tubes** (Fig. 160). Each of this tiny pair of tubes ends in a funnel-shaped enlargement which normally covers a small part of the surface of the ovary. When the egg has been discharged into the body cavity, it normally is directed into one of these funnels by currents set up by the beating of cilia which

* The ovaries alternate in releasing their eggs, but the alternation is irregular and unpredictable.

line the oviducts. Rarely, having failed to enter the oviduct, an egg is fertilized within the abdominal cavity, where, attached to some organ such as the liver, it begins to develop. Usually, when this occurs, development cannot be completed and the embryo must be removed from its position in the abdominal cavity; there have been instances, however, of such embryos completing development and being "born" by means of a surgical operation on the mother.

The two oviducts empty directly into the upper corners of a pear-shaped organ, the **uterus** or **womb**, the primary function of which is to house the developing embryo until the time of birth. This organ, which lies in the middle of the lower part of the abdominal cavity (Fig. 160), just behind the urinary bladder, is about the size of a clenched fist, and

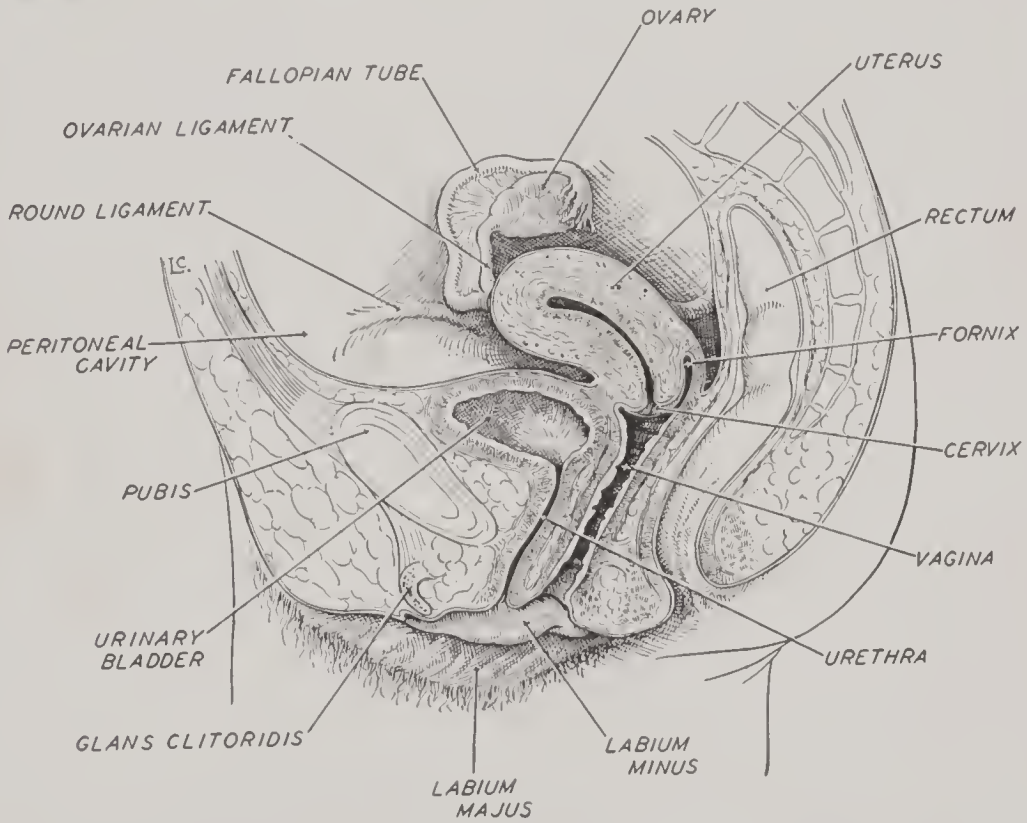


Fig. 160. Schematic sagittal section of the female pelvic region, showing the genital organs and their relations to the urinary bladder and urethra. (Turner, C. D.: General Endocrinology.)

has thick muscular walls and a mucous lining richly supplied with blood vessels. From the center of its lower end a single muscular tube, the **vagina**, passes to the outside of the body. The vagina is many times larger than any other tube previously mentioned in this chapter, since it serves both as receptacle for the sperm, and so must accommodate the penis, and as birth canal when the prenatal development is complete. The uterus terminates in a muscular ring, the **cervix**, which projects a short distance into the vagina.

The external female sex organs are collectively known as the **vulva**. At the lowest extremity of the torso, in front, is a mass of fatty tissue forming a slight elevation known as the **mons Veneris**. From this point, two folds of skin, covered with hair, the **labia majora**, extend back and down, to enclose the opening of the vagina, and grow together into a

single tissue behind it. Inside the labia majora are two other folds of skin, free of hair, the **labia minora**. At the junction of these two in front is a sensitive, erectile organ, about the size and shape of a small pea. This is the **clitoris**, an organ homologous to the penis of the male; that is, it develops from the same embryonic structure from which the penis develops, and, similarly, it contains spongy tissue capable of becoming engorged with blood during sexual excitement. Unlike the male organ, however, its only function is excitatory. Behind the clitoris is the opening of the urethra, which in the human female has only a urinary function, and behind that the much larger opening of the vagina. Before the first sexual intercourse, the latter opening is usually closed by a thin membrane, called the **hymen**, but disease or accident may destroy this in childhood.

3. Fertilization. In the act of sexual intercourse or **copulation** the erect penis is inserted into the vagina, where it ejaculates about 200,000,000 sperm. The sperm travel up the vagina and into the uterus partly under their own power and partly by force of the muscular contractions of the walls of these organs. Most of the sperm become lost on the journey, but a few find their way to the openings of the oviducts and swim up them. Sperm have the ability to swim against a current, and the same current which draws the egg from the abdominal cavity into the oviduct probably assists them in finding their way. If ovulation has occurred shortly after or before copulation, the egg which passes into the oviduct probably will be fertilized by one of the sperm. Fertilization usually occurs in the upper third of the oviduct; by the time the egg reaches the lower part of the oviduct it has lost the capacity to be fertilized. Only one of the millions of sperm deposited at each ejaculation fertilizes a single egg.

Each human egg is surrounded by a layer of cells (derived from the follicle) called the *corona radiata*, which must be pierced before a sperm is able to unite with the egg. The individual cells of the layer are held together by a complex organic substance known as **hyaluronic acid**, which is acted upon by the enzyme **hyaluronidase.** Since each sperm contains only a small amount of hyaluronidase, it requires the combined supply of several hundred thousand sperm to break down the hyaluronic acid and separate some *corona radiata* cells, in order that one sperm may enter and fertilize the egg. As soon as the egg has united with a sperm, it develops a membrane which prevents the entrance of others. The unused sperm and the unfertilized eggs die in the oviducts or uterus and are removed by white corpuscles.

Considering how many factors are working against it, it seems remarkable that fertilization ever does occur, and indeed, man is a comparatively infertile animal. The best evidence available at present indicates that sperm remain alive and retain their ability to fertilize for twenty-four to forty-eight hours at most after having been deposited in the female tract, while the egg loses its ability to be fertilized about twenty-four hours after ovulation. Thus the period during the menstrual month when fertilization can occur is brief. Moreover, the sperm cells are extremely delicate; their cytoplasm contains small resources of food, and, being sensitive to heat, they die quickly at body temperature. Still

another hazard lies in the leukocytes of the vaginal epithelium, which always engulf countless millions of sperm. It is only because copulation is so frequent and so many sperm are deposited at each ejaculation, that the human race is able to maintain itself as well as any other species.

After fertilization has occurred, the zygote, while passing down the oviduct to the uterus, begins to divide (Fig. 161). Eight to ten days

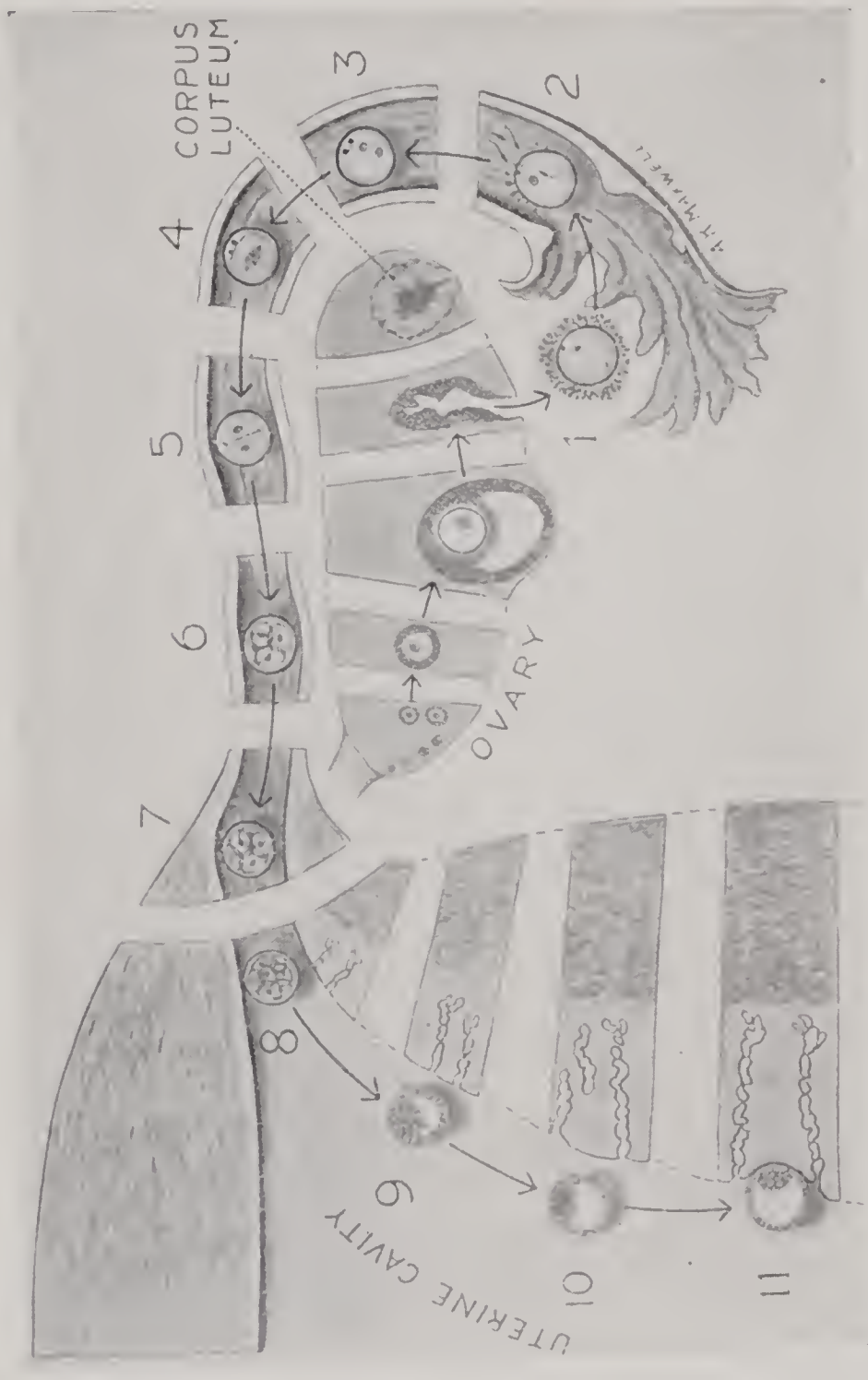


Fig. 161. Schematic representation of the maturing of an egg in the follicle of the ovary, and the release of the egg (ovulation) (*1*); the fertilization of the egg in the upper part of the oviduct (*2*); cleavage of the egg as it descends the oviduct (*3–8*); stages in the development of the embryo in the uterus before implantation (*9* and *10*); and implantation of the embryo in the wall of the uterus (*11*). (Hamilton, Boyd, and Mossman: Human Embryology, Williams & Wilkins Co., Baltimore, Md.)

elapse from the time the egg is fertilized until it is implanted in the uterine wall. Of this time, about four days are required for the passage down the oviduct; and until it is firmly implanted, the developing embryo is nourished by a secretion of the uterine glands known as "uterine milk." By the time of implantation the embryo consists of a cluster of several hundred cells derived by division from the single, original, fertilized egg.

4. Implantation. The implantation of the developing embryo in the lining of the uterus is a process that involves activity on the part of both embryo and uterine lining. The embryo secretes a substance which destroys a few of the cells of the lining and then penetrates at that point. This stimulates the uterine tissues to grow and surround the embryo. It is possible to get this imbedding reaction by pricking the lining of the uterus with a glass needle; when a rat is treated in this way, the uterus develops just as though an embryo were present and the rat undergoes a short pseudopregnancy.

5. Nutrition of the Embryo. After implantation in the uterine lining, the embryo continues to develop, at first obtaining its nourishment by chemically breaking down the cells of the uterine wall immediately around it, and later by extracting the nutritional essentials from the blood stream of the mother, via the blood vessels of the placenta.

The new human being develops only from the cells which lie along one side of the hollow ball originally implanted in the uterus; the other cells form membranes which nourish and protect the developing child and eventually form part of the "afterbirth." The problem of supplying the embryo with food during development has been solved in different ways by the several groups of vertebrates.

Fish and amphibia produce relatively large eggs, containing yolk to supply the necessary proteins, fats and carbohydrates; these eggs are laid and develop in water, whence they obtain oxygen, salt, and water itself. The embryos of these animals have a pouchlike outgrowth of the digestive tract, known as the **yolk sac,** which grows around the yolk, digests it, and makes it available to the rest of the organism.

The higher vertebrates, reptiles and birds, have developed a reproductive system involving eggs which can be laid on land. Such eggs require a hard shell to protect them from excessive drying, due to loss of water, and have additional membranes for the protection and nutrition of the embryo. The familiar "white" of the hen's egg is an extra store of protein and water to carry the embryo through to the time of hatching. Both the shell and the white of the eggs of reptiles and birds are secreted by glands located in the wall of the oviducts while the egg is passing down these tubes.

6. The Embryonic Membranes. Since the embryos of reptiles, birds and mammals do not develop in the water as their fish and amphibian ancestors did, several embryonic membranes have evolved to enfold the embryo and protect, support and nourish it. These membranes, called the **amnion,** the **chorion** and the **allantois,** are sheets of living tissue growing out of the embryo itself—the amnion and chorion out of the body wall to enfold the embryo (Fig. 162), and the allantois out of the digestive tract to function in the absorption of food.

The formation of the amnion is a complex process, differing in detail in different species, but in all it is essentially an outfolding of the body wall of the embryo which grows around the embryo to meet and fuse above it (Fig. 162). The space created between the embryo and the amnion, known as the **amniotic cavity,** becomes filled with a clear, watery fluid secreted by both the embryo and the membrane. Thus embryos of the higher vertebrates reach the birth stage enclosed in a

small pool within the shell or uterus. The amniotic fluid acts as a protective cushion which absorbs shocks and prevents the amniotic membrane from sticking to the developing embryo, while permitting the organism a certain freedom of motion. During the birth process of

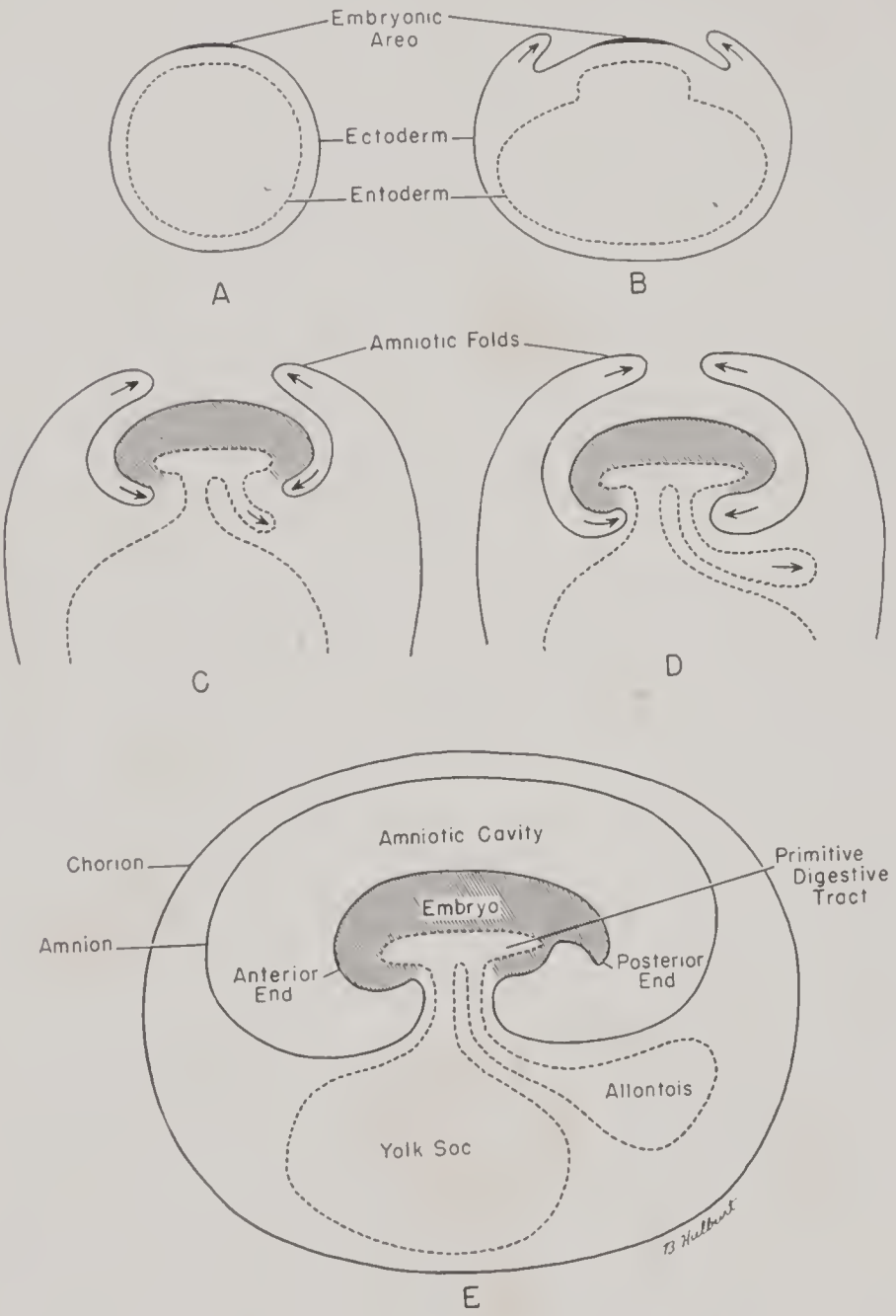


Fig. 162. Steps in the formation of the embryonic membranes—amnion, chorion, yolk sac and allantois—in a typical mammal such as a pig. Arrows indicate direction of growth and folding.

human beings, pressure of the amniotic fluid helps to dilate the neck of the uterus; later, the amnion normally ruptures, releasing, shortly before the fetus is born, about a quart of amniotic fluid, the so-called "waters." Sometimes the amnion fails to burst, and the child is born with it still enveloping its head. It is then popularly known as a "caul," and is the source of many odd superstitions.

The amnion develops from the inner part of the original fold from the body wall; the outer part forms a second membrane, the **chorion.** This membrane, in the eggs of reptiles and birds, rests in contact with

the inner surface of the shell, and in mammals it is established next to the cells of the uterine wall.

The allantois, like the yolk sac, is an outgrowth of the digestive tract. It grows between the amnion and chorion and, in animals like the chick, where it is a large and functional membrane, fills almost all the space between these two. The allantois of the chick fuses with the chorion to form a compound membrane, full of blood vessels, by means of which the embryo takes in oxygen, gives off carbon dioxide, and excretes waste products. Since the embryo "breathes" through the shell, it will suffocate if the shell is coated with wax. In the human, the allantois is small and nonfunctional, except for furnishing blood vessels to the placenta, and the yolk sac is completely nonfunctional. When the chick hatches from the shell, or when the child is born, most of the allantois and all the other membranes are discarded. But the base of the allantois, the part connected to the digestive tract originally, remains within the body and is converted into part of the urinary bladder.

As the human embryo grows, the region on the ventral side from which the folds of the amnion, the yolk sac and the allantois grew, becomes relatively smaller, and the edges of the amniotic folds come together to form a tube which encloses the other membranes. This tube is the **umbilical cord**, which contains, in addition to the yolk sac and allantois, the large blood vessels through which the embryo obtains nourishment from the wall of the uterus. The umbilical cord is composed chiefly of a peculiar jelly-like material found nowhere else. It is about half an inch in diameter and about 2 feet long. It is usually twisted spirally, and in its contortions before birth, the fetus* sometimes passes through a loop of the cord and actually ties a knot in it.

7. The Placenta. The outer surface of the chorion, in man and the higher mammals, is thin over most of its surface, but at the outer extremity of the umbilical cord it develops a number of finger-like projections, known as **villi**, which grow into the tissue of the uterus. These villi, plus the tissues of the uterine wall in which they are imbedded, make up the organ known as the **placenta**, by means of which the developing embryo obtains food and oxygen and gets rid of carbon dioxide and metabolic wastes (Fig. 163). These processes can be accomplished because of the many capillaries in the villi which receive blood from the embryo by way of one of the two umbilical arteries, and return it to the embryo by way of the umbilical vein. The part of the uterine wall which makes up the placenta is a mass of spongy tissue filled with blood which originates in the mother's blood stream. *The bloods of the mother and fetus do not mix at all in the placenta or any other place;* the blood of the fetus in the capillaries of the chorionic villi comes in close contact with the mother's blood in the tissues between the villi, but they are always separated by a membrane, through which substances must diffuse. As the embryo develops, the placenta necessarily grows too. At the time of birth, it is a thick, circular disc,

* As soon as the zygote or fertilized egg begins to divide, it is called an embryo. After the embryo has begun to resemble a human being (some two months after fertilization), it is referred to as a fetus until the time of birth.

about 7 inches in diameter, 1 inch thick, and weighing about a pound. Besides serving as the nutritive, respiratory and excretory organ of the fetus, the placenta is an important endocrine gland (see p. 328).

The uterus also increases in size as the fetus grows, and by the end of nine months its mass is twenty-four times as great as at the beginning of pregnancy. After six months of fetal development the upper end of the uterus is on a level with the navel; by eight months it is as high as the lower edge of the breastbone. Within the uterus the fetus assumes a characteristic position with elbows, hips and knees bent, arms and legs crossed, back curved, and the head bowed and turned to one side. At birth the fetus usually is turned head downwards so that its head

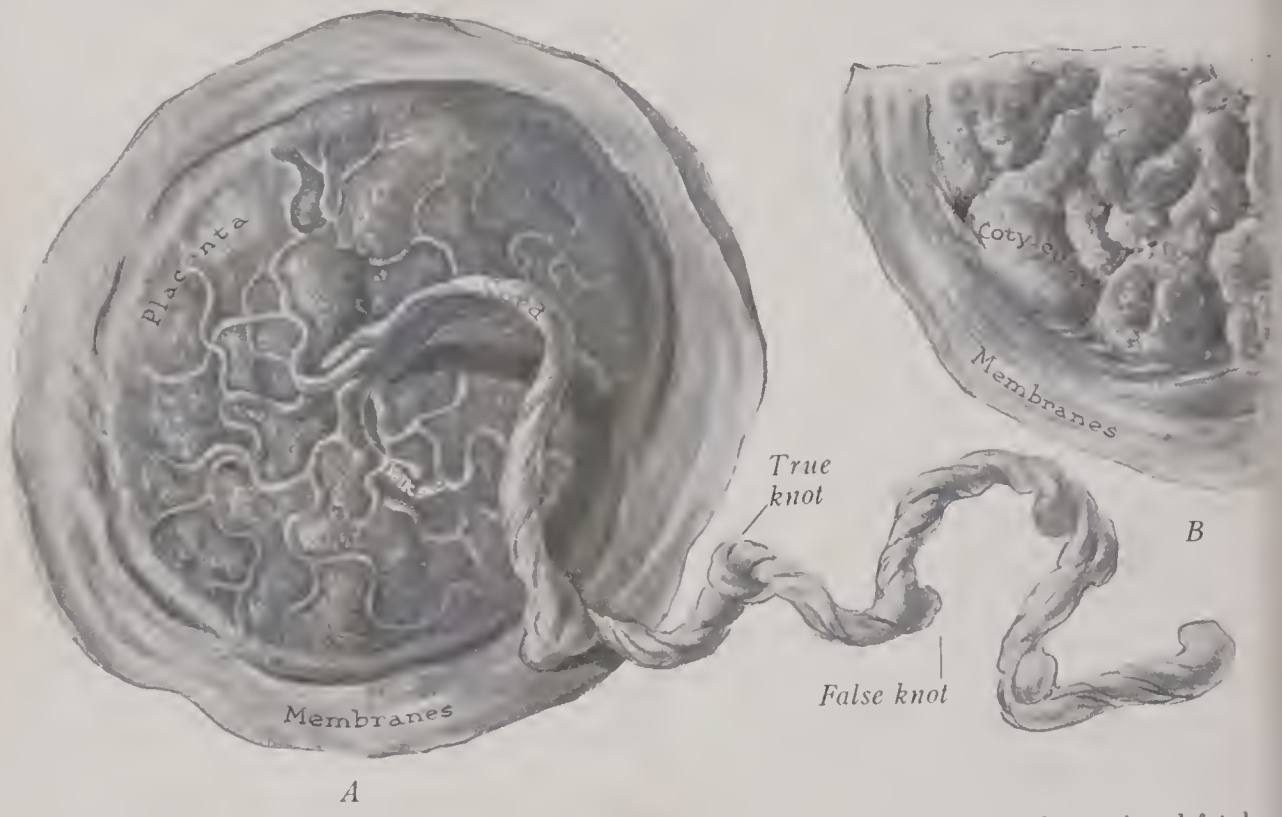


Fig. 163. The "afterbirth," consisting of the placenta, umbilical cord, and associated fetal membranes (one third natural size). *A*, View of the surface towards the fetus. *B*, Section of the surface towards the uterine wall. (Arey.)

emerges first, but occasionally the buttocks or feet are presented first, making delivery more difficult.

8. Birth. The factors which actually initiate the process of birth or **parturition** after the period of pregnancy is complete, are unknown. Childbirth begins with a long series of involuntary contractions of the uterus, experienced as "labor pains." Labor may be divided into three periods. During the first one, which lasts about twelve hours, the contractions of the uterus move the fetus down toward the cervix, and cause the latter to dilate, enabling the fetus to pass through. At the end of this period the amnion usually ruptures, releasing the amniotic fluid, which flows out through the vagina. In the second period, which normally lasts between twenty minutes and an hour, the fetus passes through the cervix and vagina and is born or "delivered" (Fig. 164). At this time, before the umbilical cord is cut, the contractions of the uterus

squeeze much of the fetal blood from the placenta back into the infant. After a few minutes the pulsations in the umbilical cord cease, and the cord is ready to be tied and cut, severing the child from the mother.

Fig. 164. Models showing the process of birth. (From the Dickinson-Belski series, the Maternity Center Association.) *A*, Head passing through the dilated cervix of the uterus into the upper part of the vagina. *B*, Head passing through opening of vagina. (Patten, B. M.: Human Embryology, The Blakiston Co.)

The stump of the cord gradually shrivels until nothing remains but the depressed scar, the **navel**. During the last stage of labor, which lasts ten or fifteen minutes after the birth of the child, the placenta and the fetal membranes are loosened from the lining of the uterus by another series

of contractions and expelled. At this stage they are called collectively the "afterbirth." In man and certain other mammals this is accompanied by some loss of blood, for part of the lining of the uterus is torn away with the afterbirth. In other mammals, where the connection between the fetal membranes and uterine wall is not so close, the placenta can pull away from the uterine wall without causing bleeding. After birth the size of the uterus decreases, while its lining is rapidly restored.

In general, women of civilized countries have more difficulty during childbirth than do the women of primitive tribes, and they frequently require artificial aid in being delivered. The physician present at birth, called an **obstetrician,** sometimes administers drugs, such as the hormone of the posterior lobe of the pituitary, to increase the contractions of the uterus, or he may have to assist the expulsion of the child by using a pair of forceps to draw it out. In some women the aperture between the pelvic bones, through which the vagina passes, is too small to permit the passage of the baby. In such cases the child must be delivered by an operation in which the abdominal wall and uterus are cut open from the front. This is the "caesarean operation," so called because Julius Caesar was reputed to have been born in this way.

In a little more than 20 per cent of all known pregnancies the infant is born before it is prepared to carry on an independent existence. When this occurs, the birth is called an **abortion** or **miscarriage.** Such births are caused by improper implantation of the embryo, by faulty functioning of the placenta, or by injury to the mother.

Among mammalian species there are great differences as to the condition of the young at birth. The newborn of some species, such as the rat, are blind, hairless and helpless, while others, such as the guinea pig, are well developed and able to walk and eat solid food. There is also great variation in the weight of the newborn in comparison to the mother's weight: a newborn polar bear weighs 0.1 per cent of its mother's weight; a newborn human weighs about 5 per cent as much as its mother; and a newborn bat may weigh as much as 33 per cent of its mother's weight.

9. Nutrition of the Infant. The enlargement of the breasts during pregnancy and the onset of milk secretion occur under the stimulus of hormones from the ovary and the anterior pituitary, but the continuation of the milk secretion depends upon the presence of a suckling child. If the newborn infant is not breast-fed, the breasts stop secreting milk after a few days and decrease in size. Otherwise, they continue to yield milk for six to nine months or even longer. Formerly, it was not infrequent for women to nurse their children for as long as a year and a half.

As everyone knows, milk is an excellent food, containing proteins, fats and carbohydrates. But it is deficient in some things, especially iron and vitamins C and D, so that at the present time an infant's diet is usually supplemented after the first month or so with eggs to supply iron, and orange juice and cod liver oil to supply the vitamins. The milk of various species differs in its content, and often it is difficult to raise a human infant on cow's milk, because the latter has more protein and less sugar than human milk. Usually, by diluting cow's milk and adding sugar to approximate the content of human milk, an acceptable formula can be made up.

QUESTIONS

1. How are eggs and sperm adapted structurally for their respective functions?
2. Distinguish between copulation and fertilization.
3. How is the seminal fluid produced?
4. Describe the movements of the egg from the time it is released by the ovary.
5. Trace the path of a sperm from the testis to its union with the egg.
6. What are the amnion, chorion and allantois?
7. How is the umbilical cord formed?
8. What is the "afterbirth?"

SUPPLEMENTARY READINGS

Kimber, D. C., Gray, C. E., and Stackpole, C. E.: *Textbook of Anatomy and Physiology.* 11th ed. New York, The Macmillan Company, 1942.

A complete but elementary description of the anatomy and physiology of human reproduction.

Parshley, H. M.: *The Science of Human Reproduction.* New York, W. W. Norton & Company, Inc., 1933.

A detailed, readable account of the reproductive process in man.

CHAPTER 21

EMBRYONIC DEVELOPMENT

ONE OF the most remarkable of all biological phenomena is the division and growth of a fertilized egg into the wonderfully complex, interdependent system of organs which is the adult animal. The wonder lies not only in the fact that the organs are complicated and are reproduced in each new individual with such fidelity, but that many of them begin to function while they are still developing. The fetal heart, for instance, begins to beat during the fourth week, long before its development is complete.

The science of embryology has been based upon developmental studies of such animals as the chick, frog and monkey, for until recently no early human embryos were available for study. At the present time the earliest to have been studied was ten days old, taken approximately two days after implantation. It is believed that earlier human development is probably much like the monkey's, whose embryology is well delineated.

Although, in the primary stages, the development of all multicellular animals is similar, that of the human and other primates is marked by certain peculiarities due to the embryo's being surrounded at an early time by the uterine wall. Also, in the primate, the embryonic membranes—the amnion, chorion and allantois—form and begin to function precociously.

1. Types of Eggs. One important factor in determining the type of development is the amount of yolk or stored food present in the egg, since the yolk, being nonliving and inert, will modify the processes of development in the surrounding cytoplasm.

Probably the most primitive kind of egg is that with a small amount of yolk distributed more or less evenly throughout the cytoplasm. Such eggs, known as **isolecithal** (meaning "equal yolk"), are found in such animals as the sea urchin and the primitive, wormlike marine chordate, amphioxus.

Another type of egg, produced by fish, amphibia, reptiles and birds, has a large amount of yolk massed toward the lower or so-called **vegetal pole** of the egg, while the cytoplasm is concentrated toward the upper or **animal pole**. Such eggs, known as **telolecithal** (meaning "end yolk"), differ in the amount of yolk present. The frog's egg is about half yolk, whereas the hen's egg is more than 95 per cent yolk, with its cytoplasm restricted to a small disc at the animal pole.

Mammalian eggs, although small and relatively free from yolk (Fig. 165), so that superficially they resemble isolecithal eggs, develop more nearly like telolecithal ones, probably because mammals descended from reptiles which laid the latter kind. The loss of the yolk from mammalian

eggs is a result of the fact that the yolk is no longer needed to nourish the developing embryo.

2. Cleavage. The process by which any single, fertilized egg develops into a many-celled embryo is called **cleavage,** indicating that it actually splits or divides. This division, called **mitosis,** is accompanied by a complicated series of processes *within* the nucleus and cytoplasm of the

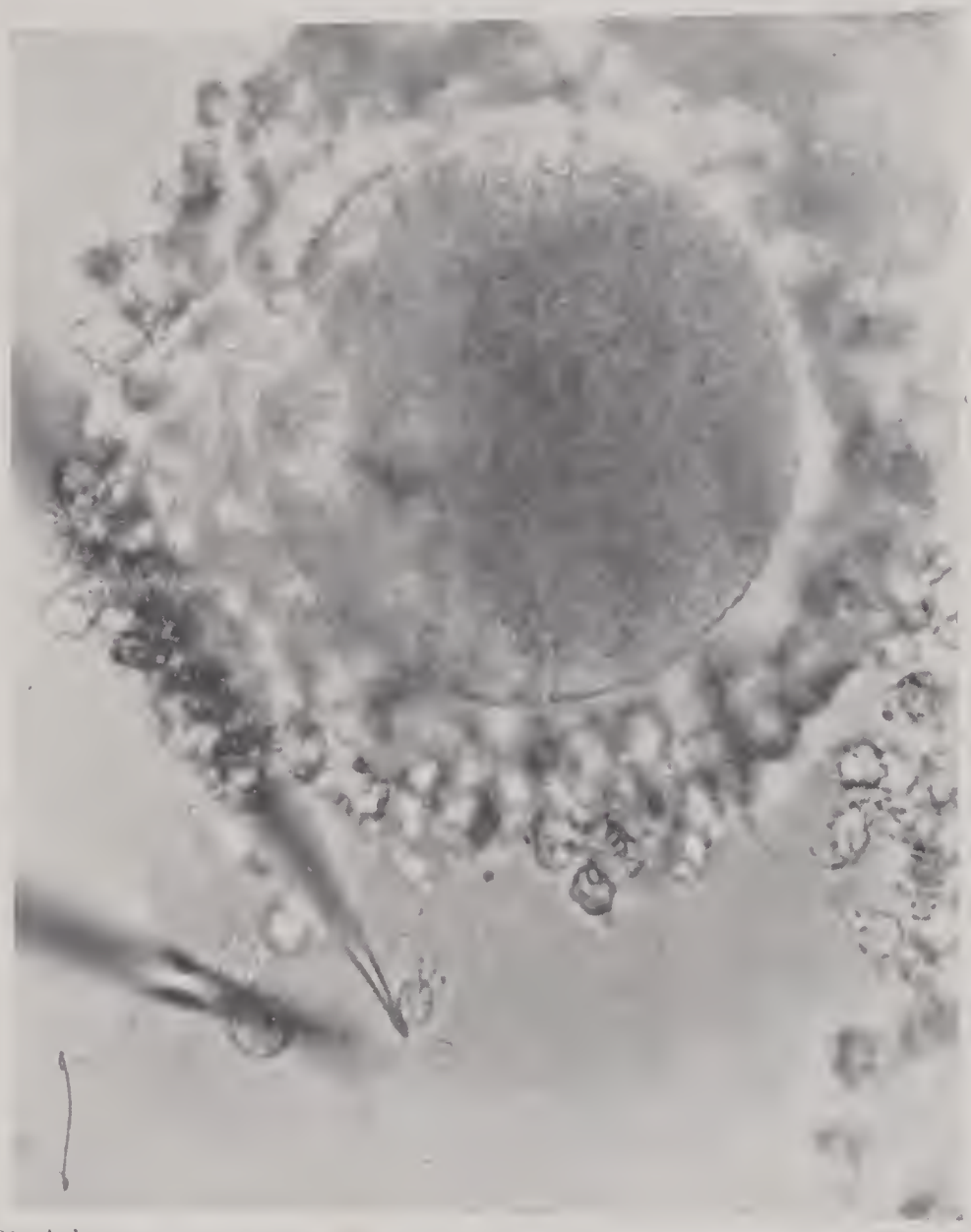


Fig. 165. A human egg recovered from the oviduct. The large egg cell is surrounded by the many small cells which make up the "corona radiata"—cells which were originally part of the follicle. The photograph was made in the course of an experiment in which tiny needles were used to dissect away the corona radiata cells and to dissect the egg itself. The two needles can be seen in the lower corner of the picture, dissecting the nucleus out of one of the corona radiata cells. (Magnified 600 times.) (Courtesy of Dr. William R. Duryee.)

cells, which will be considered in the chapter on heredity. For the time being we shall be concerned only with the larger, *external* changes brought about by cleavage.

When a simple, isolecithal egg is fertilized, it divides by mitosis to form a two-celled embryo. The line of this first division passes through both the animal and vegetal poles of the egg, splitting it down the center into two equal cells (Fig. 166). This is followed by a second cleavage division, also passing through both poles of the cells (now

called an **embryo**), but at right angles to the first, which divides the two cells into four. The third division is a horizontal one, at right angles to the other two divisions, which splits the four cells into eight—four above and four below the line of cleavage. Further divisions divide these eight cells into thirty-two, sixty-four, 128 and so on, but the later divisions are usually somewhat irregular. Each of the cells formed by cleavage is exceedingly small, and the total mass of all the cells is less than the mass of the original fertilized egg, because some of the stored food is used up in the process.

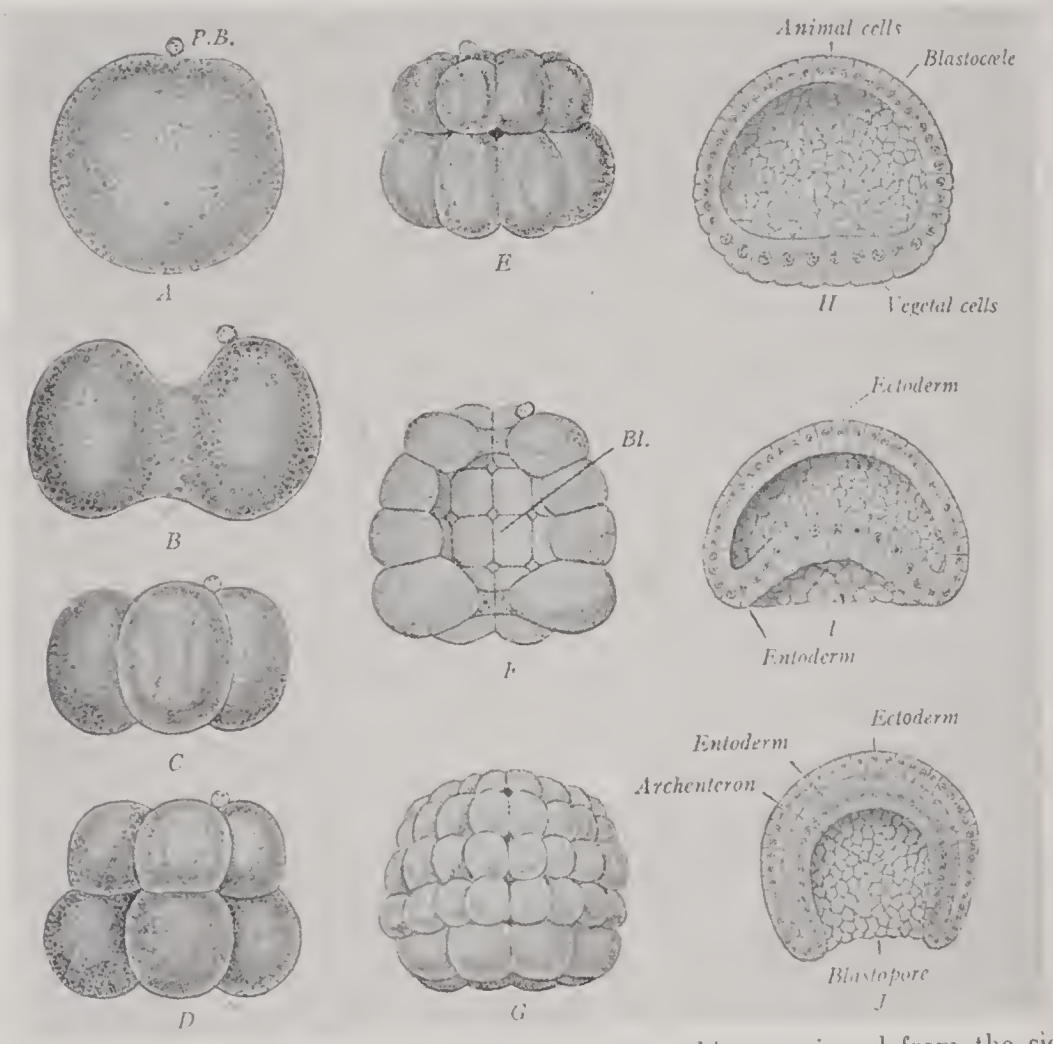


Fig. 166. Isolecithal cleavage and gastrulation in Amphioxus, viewed from the side. *A*, Mature egg with polar body (P.B.). *B*, Two-cell stage. *C*, Four-cell stage. *D*, Eight-cell stage. *E*, Sixteen-cell stage. *F*, Thirty-two-cell stage, cut open to show the blastocoele (Bl.). *G*, Blastula. *H*, Blastula cut open. *I*, Early gastrula, showing invagination of vegetal pole cells. *J*, Late gastrula, invagination completed. (Arey.)

3. Blastula Formation. As the cells undergo further division, a spherical mass is formed, in the center of which a cavity appears. With additional cleavages the cavity increases in size, until finally the embryo consists of several hundred cells, arranged in the form of a hollow ball. At this stage the embryo is called a **blastula** (Fig. 166), and the cavity in the center, filled with fluid, is known as the **blastocoele**. The wall of the blastula consists of a *single* layer of cells.

4. Gastrulation. Almost as soon as the single-layered blastula is formed, it begins to change into a double-layered form called a **gastrula.** In simple, isolecithal eggs, gastrulation occurs by the pushing in (in-

vagination) of a section of one wall of the blastula (Fig. 166). The pushed-in wall eventually meets the opposite wall, so that the original blastocoele is obliterated. The new cavity of the gastrula is known as the **archenteron** (meaning primitive gut), because it forms the rudiment of what is to become the digestive system. This opens to the outside by the **blastopore,** which marks the place where the indentation for gas-

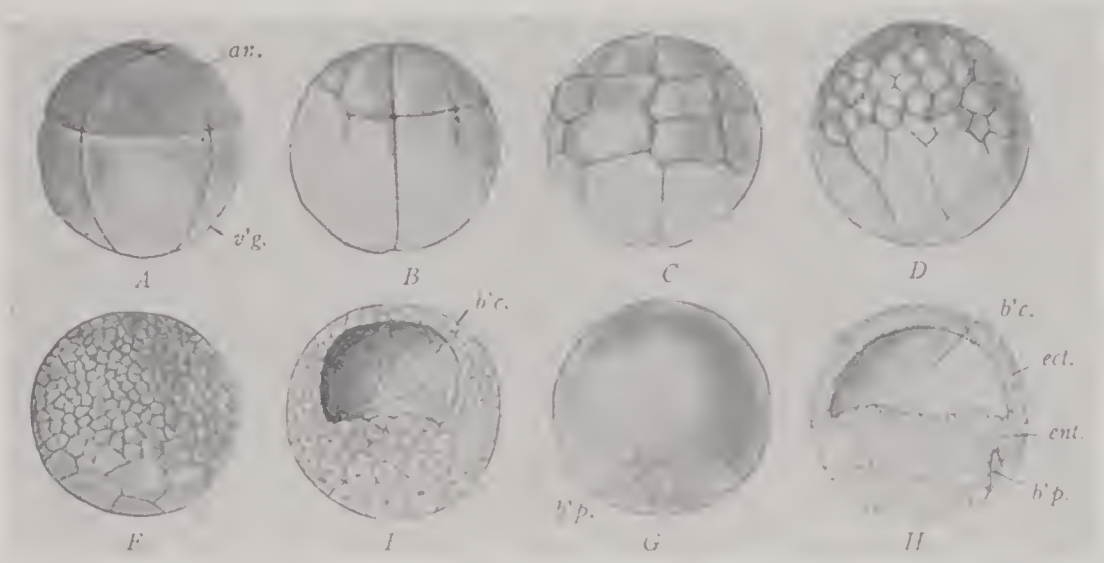


Fig. 167. Telolecithal cleavage and gastrulation in the frog, viewed from the side. *A–D*, Stages in cleavage. *E*, Blastula. *F*, Blastula cut open to show blastocoele (bc.). *G*, Early gastrula (bp. blastopore). *H*, Early gastrula cut open (ect = ectoderm; ent = entoderm, bc. = blastocoele; bp = blastopore). (Arey.)

trulation began. The formation of the two-layered embryo is accompanied by rapid growth and division of the cells, and the resulting gastrula is about the same diameter and shape as the blastula from which it came.

The outer of the two walls of the gastrula is called the **ectoderm** (outer skin); it eventually gives rise to the skin and nervous system. The inner wall, lining the archenteron, is known as the **entoderm** (inner skin); it

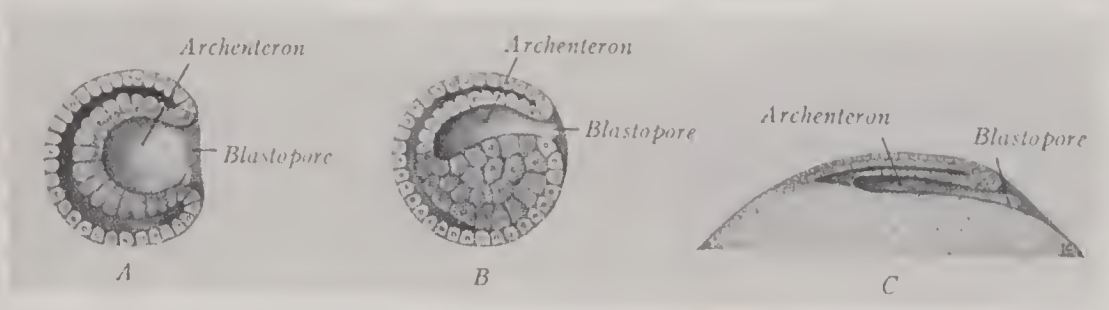


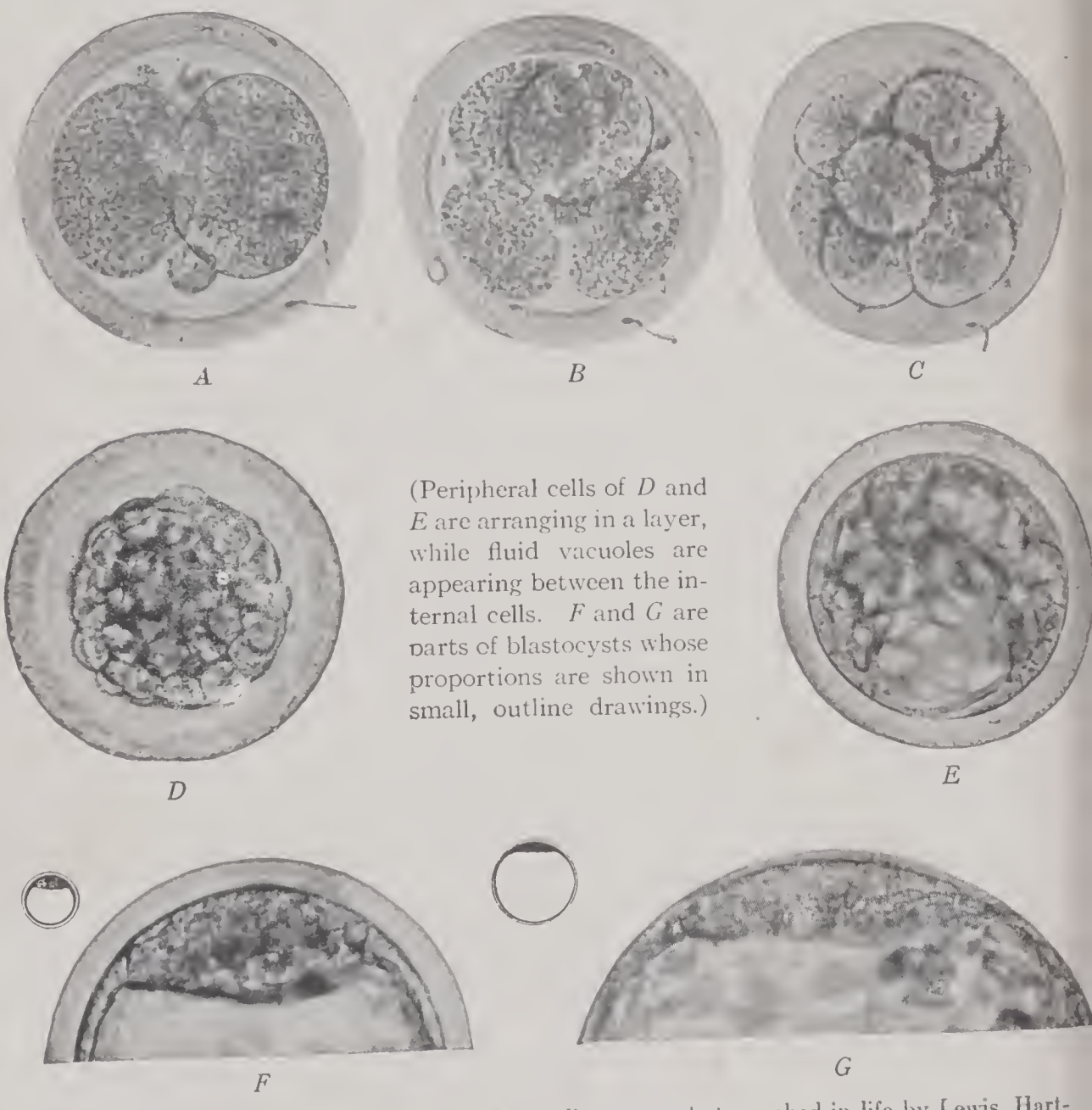
Fig. 168. Comparison of the process of gastrulation. *A*, Amphioxus. *B*, Amphibia. *C*, Bird. (Arey.)

finally becomes the digestive tract, and its outgrowths—the liver, lungs and pancreas.

5. Cleavage and Gastrulation in Frog and Chick Eggs. The processes of cleavage and gastrulation are markedly modified by the presence of large amounts of yolk: the cleavage divisions of the cells originating from the lower part of the frog's egg are slowed up by the presence of the inert yolk, with the result that the blastula consists of many small cells at the animal pole and a few large cells at the vegetal pole (Fig.

167). This means that the lower wall is much thicker than the upper wall and the blastocoele is displaced upward.

Cleavage divisions of the hen's egg occur only in a small disc of cytoplasm at the animal pole, the lower, yolk-filled part of the egg never undergoing cleavage at all. The blastocoele formed is a shallow cavity under the dividing cells (Fig. 168). In both frog and chick, gastrulation does occur, with the resulting formation of an archenteron, but the yolk



(Peripheral cells of *D* and *E* are arranging in a layer, while fluid vacuoles are appearing between the internal cells. *F* and *G* are parts of blastocysts whose proportions are shown in small, outline drawings.)

Fig. 169. Stages in the cleavage of mammalian eggs, photographed in life by Lewis, Hartman and Gregory. *A–C*, Two-, four- and eight-cell stages in the monkey. *D–G*, Later stages in the rabbit, forty-five to eighty hours after ovulation. (Arey.)

greatly modifies the simple process of invagination exhibited by the isolecithal egg.

6. Cleavage and Gastrulation in the Human Egg. The early cleavage of the mammalian egg (Fig. 169) resembles that of amphioxus in forming a cluster of cells. After this the mammalian egg differs in that the mass of cells divides into two parts—an outer, hollow sphere of cells and, attached to one side of this, an inner, solid ball of cells. The outer

sphere is the fetal membrane, the chorion, which must form at this early stage in development to unite with the maternal tissue of the uterus as implantation occurs. The embryo and the other embryonic membranes develop from the inner, solid ball of cells.

The inner ball proceeds to form a gastrula, consisting of ectoderm and entoderm, but the process is quite different from that in the lower vertebrates. Within the inner cell mass, two cavities form simultaneously (Fig. 170, *B*). The upper one is the cavity of the amnion, lined with ectoderm. The lower one is the cavity of both the yolk sac and the primitive gut, lined with entoderm. Between the two cavities the cells spread out in the shape of a flat, two-layered plate, from which the embryo develops.

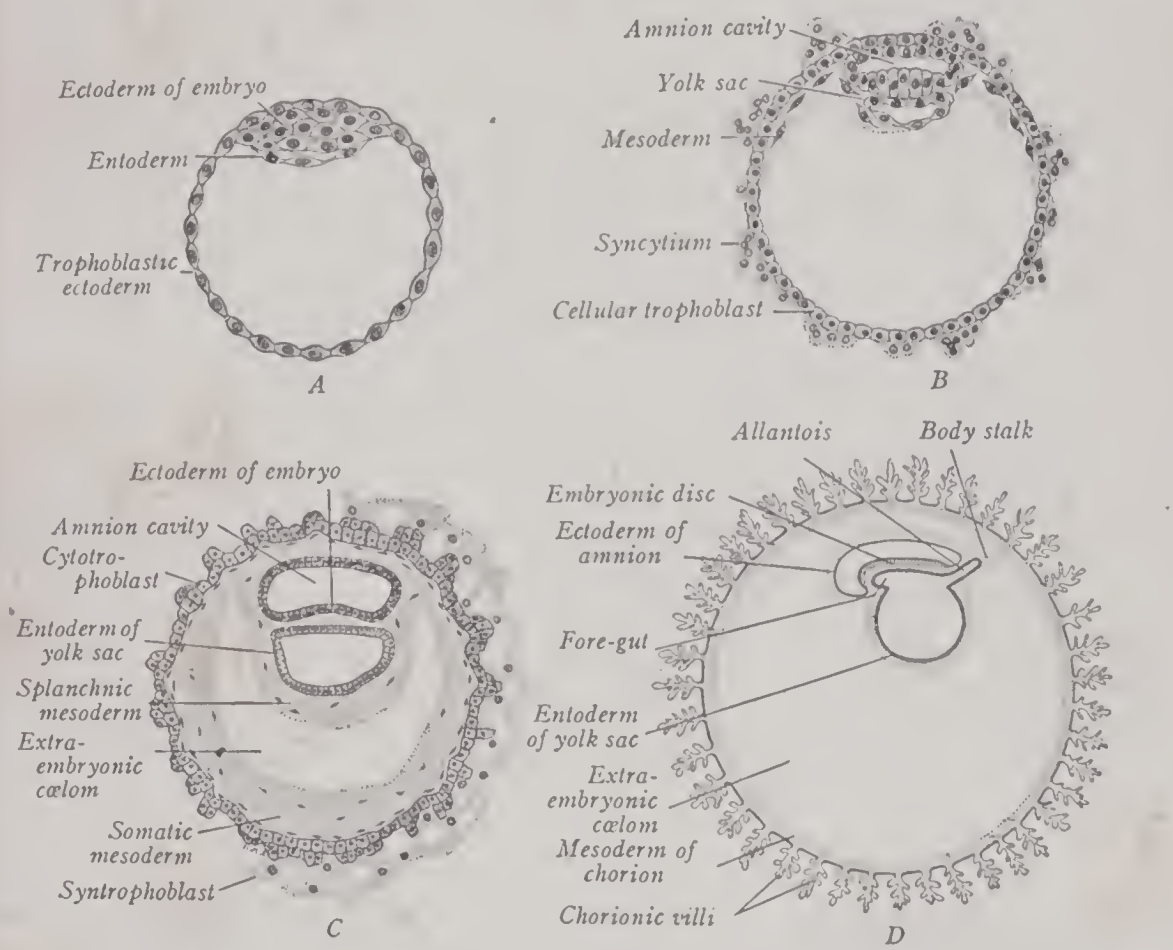


Fig. 170. Diagrams of sections through human embryos of ten to twenty days, showing the formation of the amniotic and yolk sac cavities, and the origin of the embryonic disc. (Arey.)

At what is to become the posterior end of the embryo this plate connects with the outer chorion by a group of cells known as the **body stalk** (Fig. 170, *D*). Into this body stalk grows the (nonfunctional) allantois, which has developed as a tube from the rear end of the entodermal (yolk) sac. Thus we find, after about two weeks of development, that the human embryo consists of a flat, two-layered disc, about $\frac{1}{100}$ inch across, and a stalk which connects the disc with the outer chorion.

7. Mesoderm Formation. In all animals (except sponges and coelenterates) a third layer of cells, the **mesoderm,** develops between the ectoderm and entoderm. The method of forming this layer is quite different in various species. In amphioxus it forms as a series of bilateral pouches from the entoderm, which quickly lose their connection with the

latter and fuse to form a connected layer (Fig. 171). The cavity of the original pouches remains as the celom or body cavity.

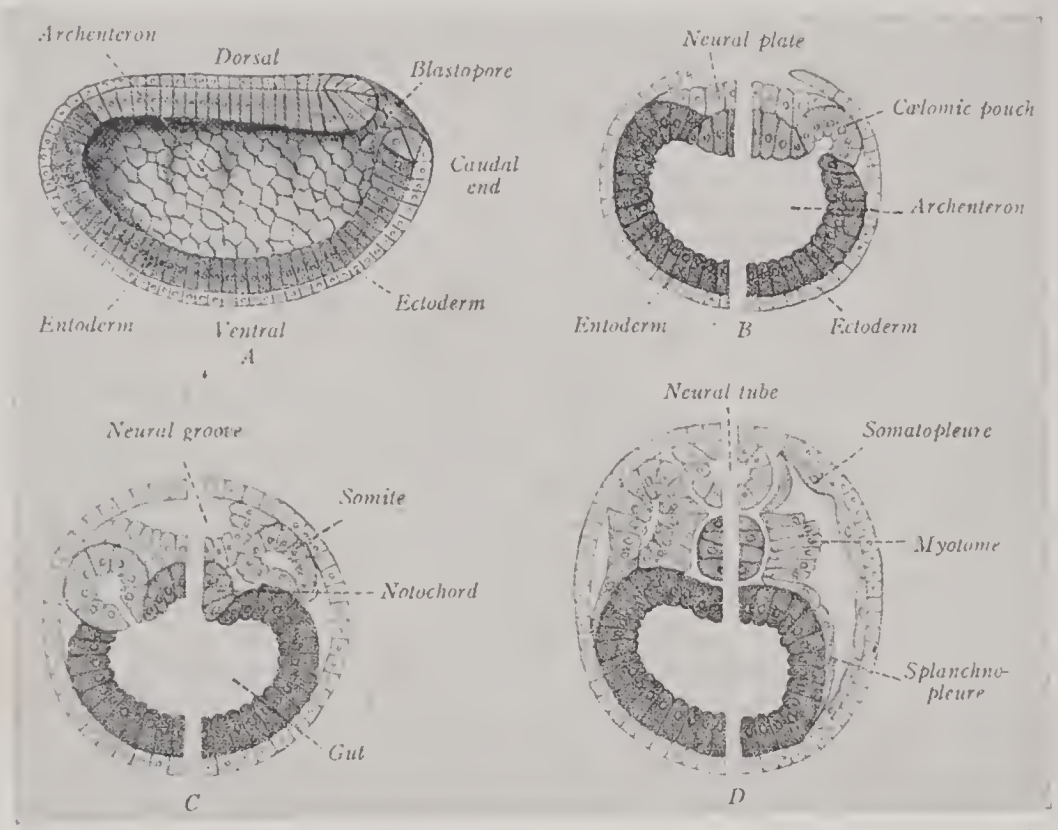


Fig. 171. Diagram illustrating the origin of the mesoderm in Amphioxus, by the budding of pouches from the primitive gut. *A*, Sagittal section of early larva. *B–D*, Cross sections, showing six successive stages in mesoderm formation. (Arey.)

In the frog embryo some of the mesoderm forms from the entoderm of the roof of the archenteron, but the major part of it is formed at the upper lip of the blastopore, where ectoderm and entoderm meet (Fig.

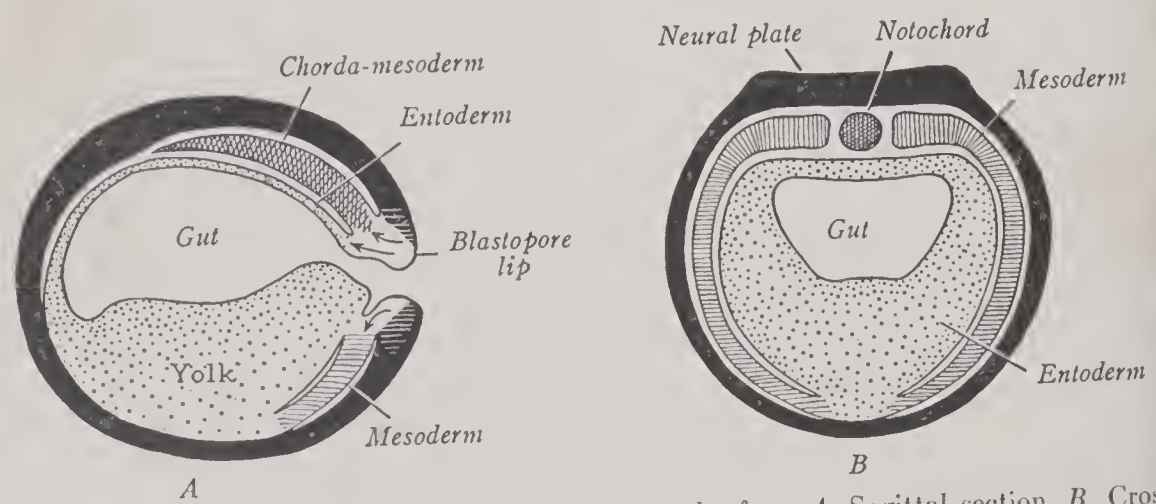


Fig. 172. Origin of the notochord and mesoderm in the frog. *A*, Sagittal section. *B*, Cross section. (Arey.)

172). This region is one of especially active proliferation of cells and also gives rise to some additional ectoderm and entoderm.

In the chick embryo, where the presence of so much yolk prevents invagination and the formation of a true blastopore, and in mammals,

where no blastopore forms, a structure known as the **primitive streak** forms on the gastrula. In the human embryo the primitive streak (Fig. 173) is a thickened band of ectoderm and entoderm layers extending forward from the body stalk, marking the longitudinal axis of the body. When cells of this band proliferate, some migrate out laterally between the ectoderm and entoderm layers to form the mesoderm. The primitive streak is a center of growth for ectoderm and entoderm as well as for mesoderm, and apparently in some way determines the position and order of appearance of the various parts of the embryo. In front of the anterior end of the streak, the head and trunk develop. The streak itself does not increase in length, but gradually decreases as the rest of the embryo grows, until it finally disappears in the tail region.

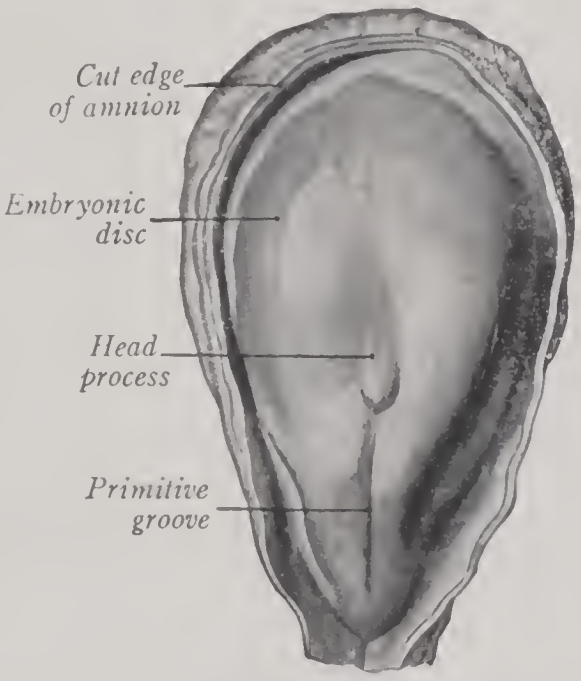


Fig. 173. A human embryo in the primitive streak stage. The head end is uppermost. The beginning of the body stalk, which attaches the embryo to the surrounding chorion, is at the bottom of the photograph. (Arey.)

Regardless of how the mesoderm originates, it splits into two sheets which grow laterally and anteriorly between the ectoderm and entoderm; one of these sheets attaches itself to the ectoderm, the other to the entoderm. The cavity between the two mesodermal sheets becomes the celom or body cavity, and when the digestive tract becomes separated as a tube from the yolk sac cavity, the mesoderm grows around it (Fig. 174). The layer of mesoderm associated with the ectoderm forms the muscles of the body wall, and the mesodermal sheet associated with the entoderm forms the muscles of the digestive tract. The entoderm itself forms only the *inner lining* of the digestive system.

8. The Notochord. The notochord is a flexible, unsegmented, skeletal rod which extends longitudinally along the dorsal midline of all chordate embryos* and is formed at the same time as the mesoderm. Its exact method of formation differs from species to species, as does that of the

* The name chordate refers to all animals having notochords, including the vertebrates and three small groups of marine, wormlike animals which have notochords but no vertebrae. Amphioxus is one of the latter.

mesoderm. In amphioxus it is formed from the entoderm as a bud, like those which produce the mesodermal pouches. It lies dorsal to the gut and just below the developing nervous system. In the chick and mammals it forms as an anterior outgrowth of the primitive streak. In all vertebrates the notochord is a short-lived structure, eventually replaced by the vertebral column, but in some lower vertebrates remnants of it can be found between the vertebrae even in adult animals.

9. Development of the Nervous System. Although the two-week old human embryo is a simple flat disc, the two-month embryo has nearly

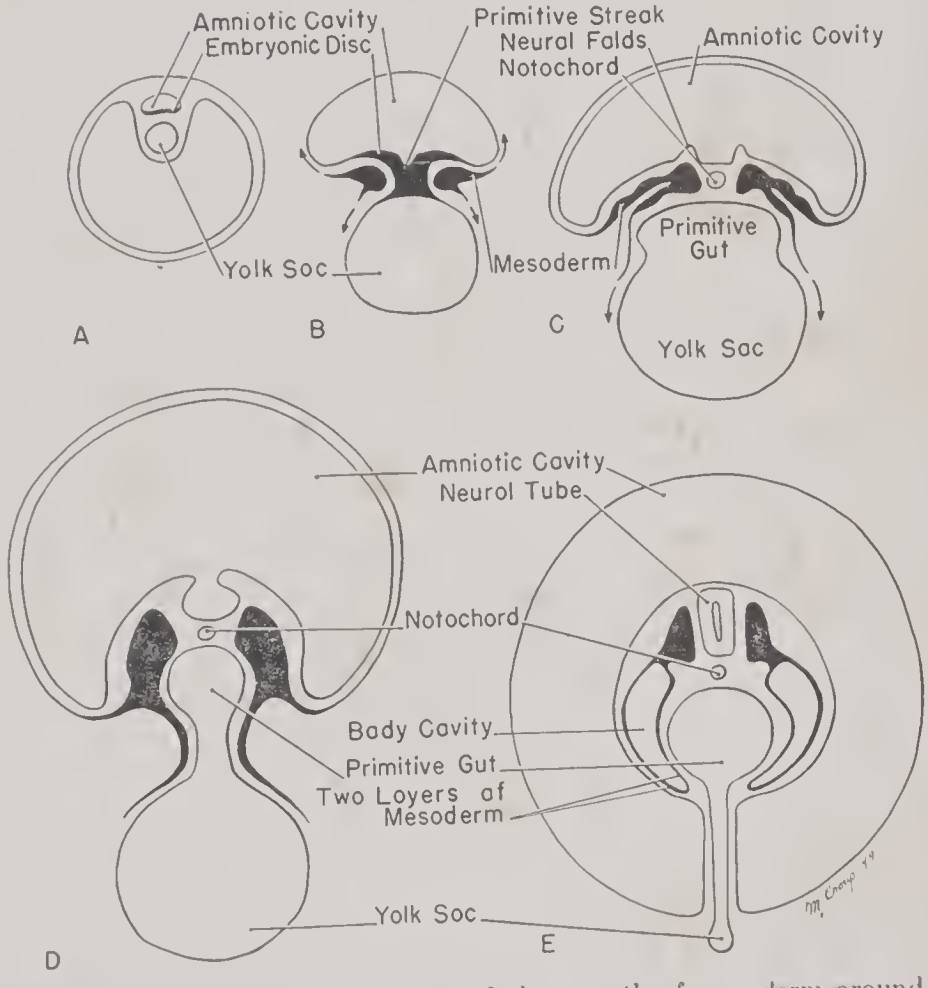


Fig. 174. Stages in the origin of body form and the growth of mesoderm around the digestive tract in man.

all its structures in rudimentary form. We shall now consider how the brain and spinal cord, which are among the earliest organs to appear, come into existence. At about the third week the ectoderm just over the notochord in front of the primitive streak develops a thickened plate of cells called the **neural plate.** The center of this becomes depressed, and is known as the **neural groove** (Fig. 175), while the outer edges of the plate rise in two longitudinal neural folds which meet at the anterior end and appear, when viewed from above, like a horseshoe. Gradually, these folds come together at the top, forming a hollow neural tube. The cavity of the anterior part of this neural tube becomes the ventricles of the brain, while the cavity of the posterior part becomes the neural canal, running the length of the spinal cord. The brain region is the first to form, and the long spinal cord develops slightly later.

The anterior part of the neural tube, which gives rise to the brain, is much larger than the posterior part, and continues to grow so rapidly that the head region comes to bend down at the front end of the embryonic disc. All the regions of the brain—forebrain, midbrain and hindbrain—are established by the fifth week of development, and a week or two later the outgrowths which will form the large cerebral hemispheres begin to grow.

The various motor nerves of the body grow out of the brain or spinal cord but the sensory nerves have a separate origin. When the neural folds fuse to form the neural tube, bits of nervous tissue, known as the **neural crest,** are left over on each side of the tube (Fig. 175). These migrate downward from their original position and form the dorsal root ganglia of the spinal nerves and the sympathetic ganglia. From cells in the dorsal root ganglia grow sensory nerves sending dendrites out to the sense organs, and axons in to the spinal cord.

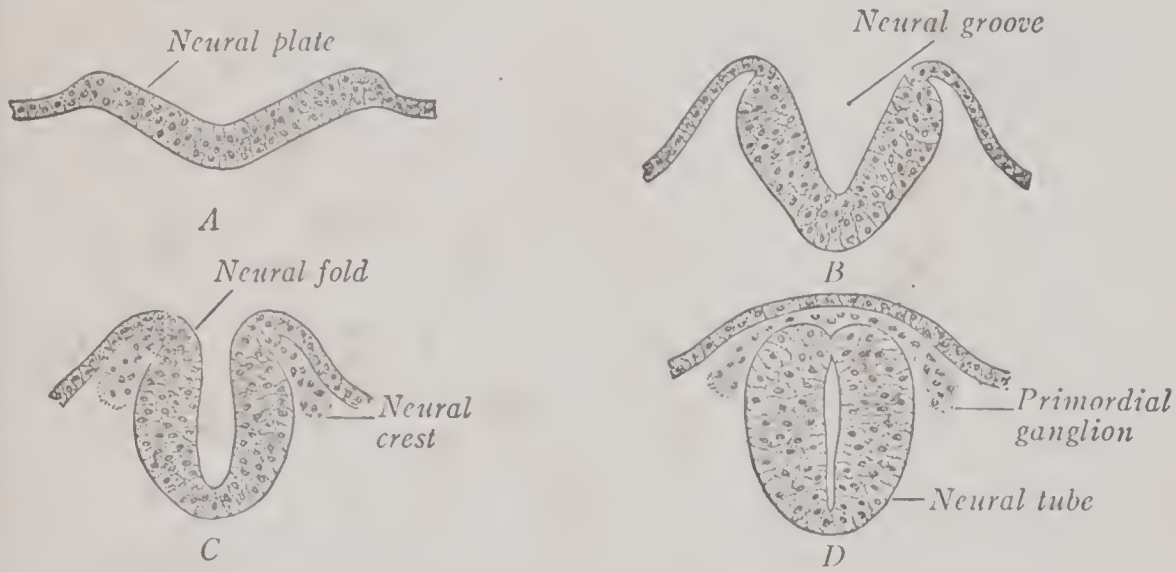


Fig. 175. The origin of the neural tube and the neural crest (which forms the ganglia of the dorsal roots and the sympathetic nerves), as shown by cross sections from human embryos of successively later stages. (Arey.)

10. The Development of Body Form. The conversion of the two-week-old flat disc into a roughly cylindrical embryo is accomplished by three processes: (*a*) the growth of the embryonic disc, which is more rapid than the growth of the surrounding tissue; (*b*) the underfolding of the embryonic disc, especially at the front and hind ends; and (*c*) the constriction of the ventral body wall to form the future umbilical cord.

Growth is rapid at the front end of the embryonic disc, and soon the head region bulges forward from the original embryonic area (Fig. 176). The tail, which even human embryos have at this stage, bulges to a lesser extent over the posterior end. The sides of the disc grow downward, eventually to form the sides of the body. The embryo becomes elongated, because growth is more rapid at the head and tail ends than laterally. The enlarging of the embryo has been compared to the increase of size in a soap bubble blown from a pipe, which, as it grows, swells out in all directions above the mouth of the pipe (the yolk sac). What is to become the mouth and heart originally lies in front of the embryonic disc, and as the disc grows and bulges over the tissues in front, the

mouth and heart swing underneath to the ventral side (Fig. 177). A similar underfolding occurs at the posterior end. By such growth and

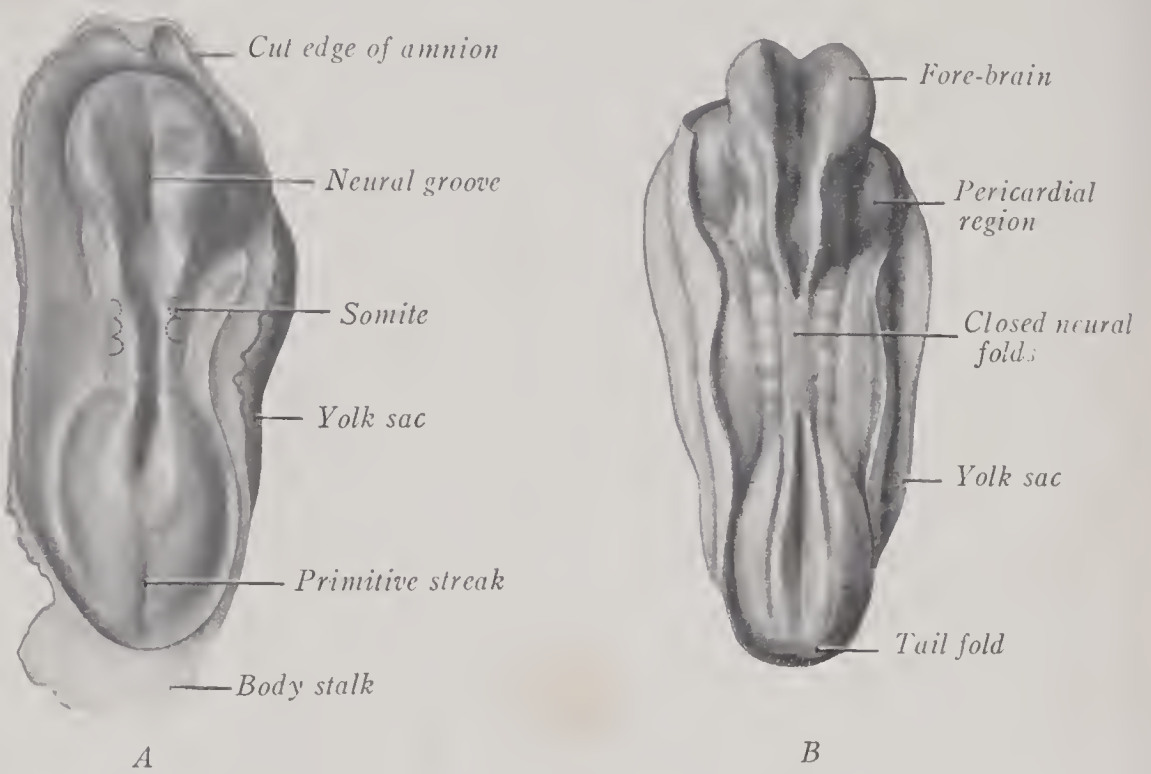


Fig. 176. Dorsal views of two human embryos about twenty-one days old. *A*, The Ingalls embryo, 1.4 mm. long, and *B*, the Payne embryo, 2.2 mm. long. (Arey.)

underfoldings the lateral and eventually the ventral walls of the body are formed, and the embryo becomes more or less cylindrical in shape.

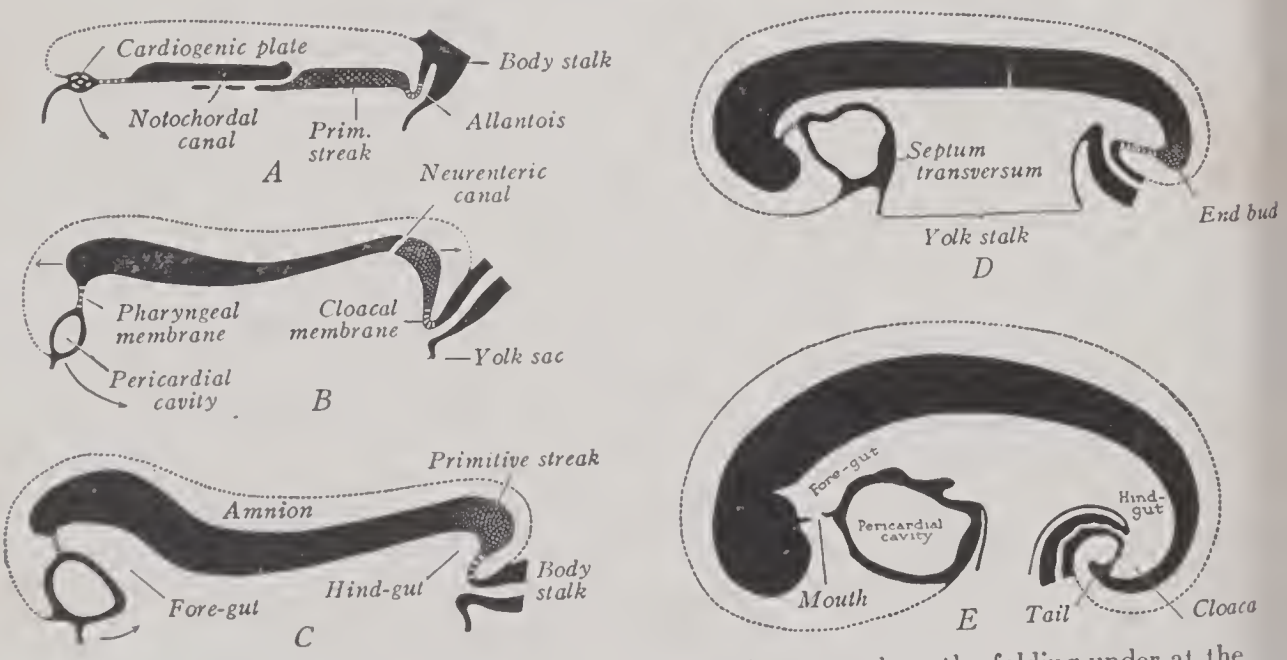


Fig. 177. Schematic, sagittal sections of human embryos to show the folding-under at the anterior and posterior ends of the embryonic disc, by means of which the body is delineated and the digestive system (foregut and hindgut) established. The arrows indicate the direction of growth. (Arey.)

While the embryo is still a simple disc, its entire under surface is open to the yolk cavity, and, as the body wall folds, a foregut and a hindgut (which form, respectively, the anterior and posterior parts of the di-

gestive tract) are cut off from the yolk sac. But they remain connected to it by the yolk stalk. As the embryo grows and folds, the amnion also grows to enclose it, finally constricting the yolk stalk and the body stalk (with its allantois and blood vessels) together into a single cylindrical tube, the **umbilical cord.** This takes place about four weeks after development is commenced, and allows the embryo to float free in the liquid-filled amniotic cavity, connected to the chorion and placenta only by the umbilical cord (Fig. 178).

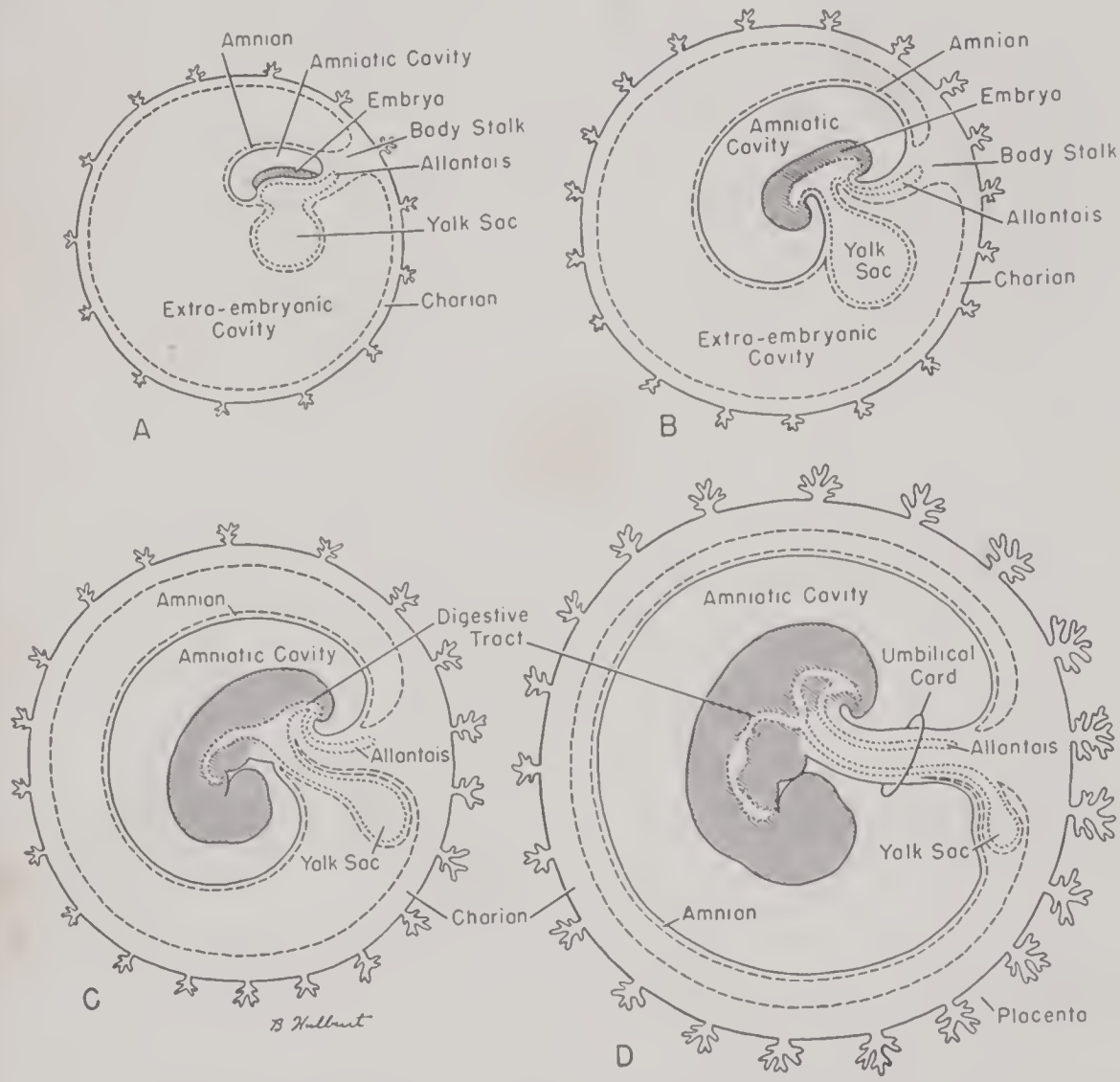


Fig. 178. Stages in the development of the umbilical cord and body form in the human embryo. The solid lines represent layers of ectoderm; the dashed lines, mesoderm; and the dotted lines, entoderm.

The month-old embryo, which is about one-fifth of an inch long, is now recognizable as a vertebrate of some kind. It has become cylindrical, with a relatively large head region, and with prominent gills and a tail. Meanwhile, blocks of muscle, known as **somites,** are forming rapidly in the mesoderm on either side of the notochord, and the beating heart is present as a large bulge on the ventral surface behind the gills. The arms and legs are still mere buds on the sides of the body.

By the end of six weeks the embryo is about half an inch long; the head begins to be differentiated; the arms and legs have grown out, but the tail and gills are still present.

At the end of two months of growth, when the embryo is an inch long,

it begins to look definitely human. The face has begun to develop, showing the rudiments of eye, ear and nose. The arms and legs have devel-

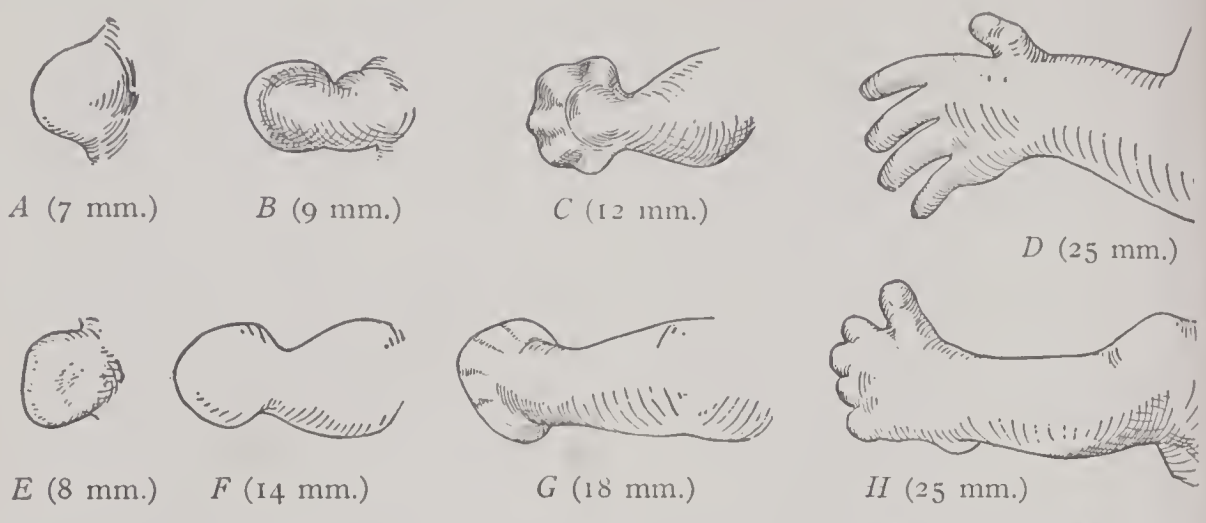


Fig. 179. Stages in the development of the human arm (upper row) and leg (lower row), between the fifth and the eighth weeks. (Arey.)

oped, at first resembling tiny paddles, but by this stage with the beginnings of fingers and toes (Fig. 179). The tail, which was prominent

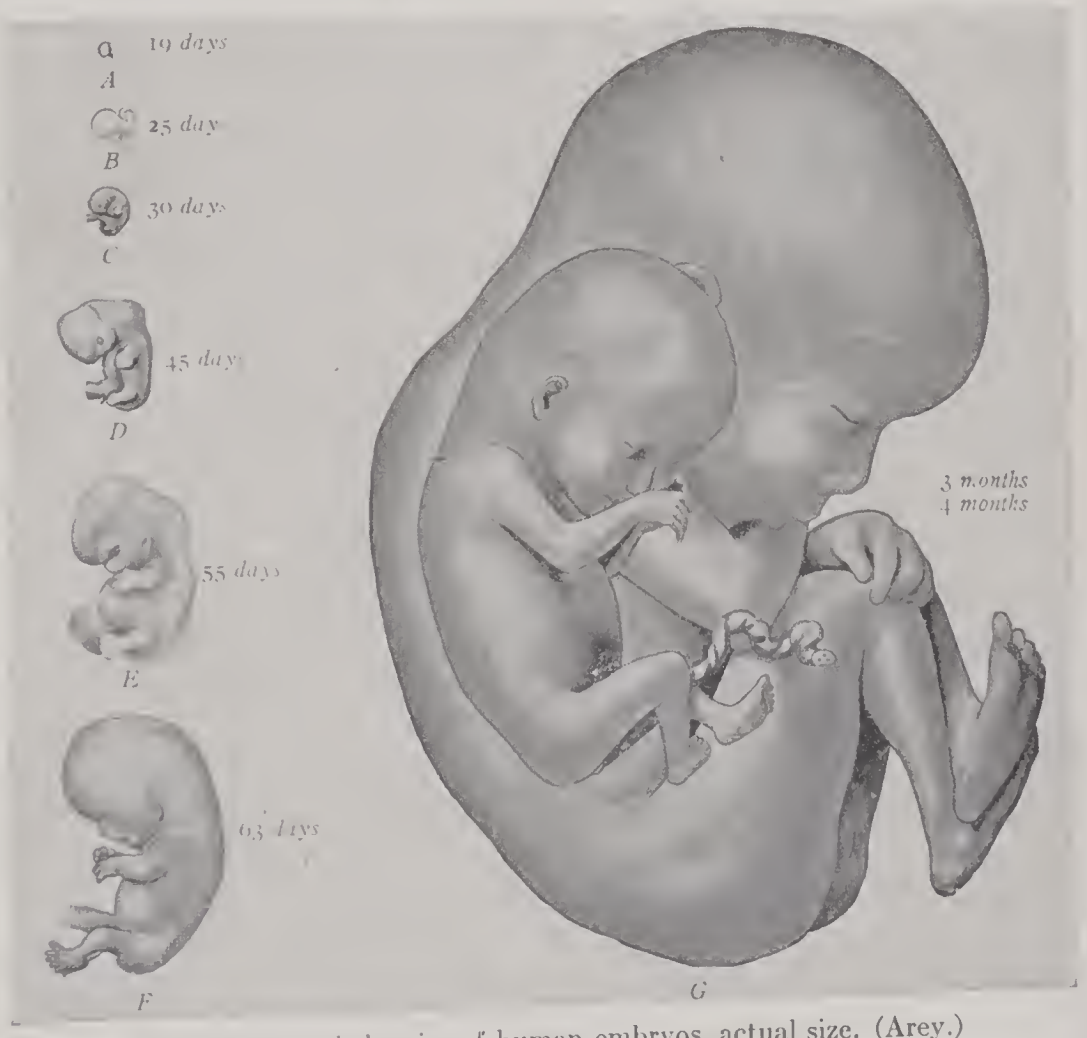


Fig. 180. A graded series of human embryos, actual size. (Arey.)

during the fifth week of development, has begun to shorten and to be concealed by the growing buttocks. As the heart moves posteriorly on

the ventral side, and the gill pouches become less conspicuous, a neck region appears. Now most of the internal organs are well laid out, so that development in the remaining seven months consists mostly of an increase in size and the completion of some of the minor details of organ formation (Fig. 180).

The embryo is about 3 inches long after three months of development, 10 inches long after five months, and 20 inches long after nine months. During the third month the nails begin forming and the sex of the fetus can be distinguished. By four months the face looks really human; by

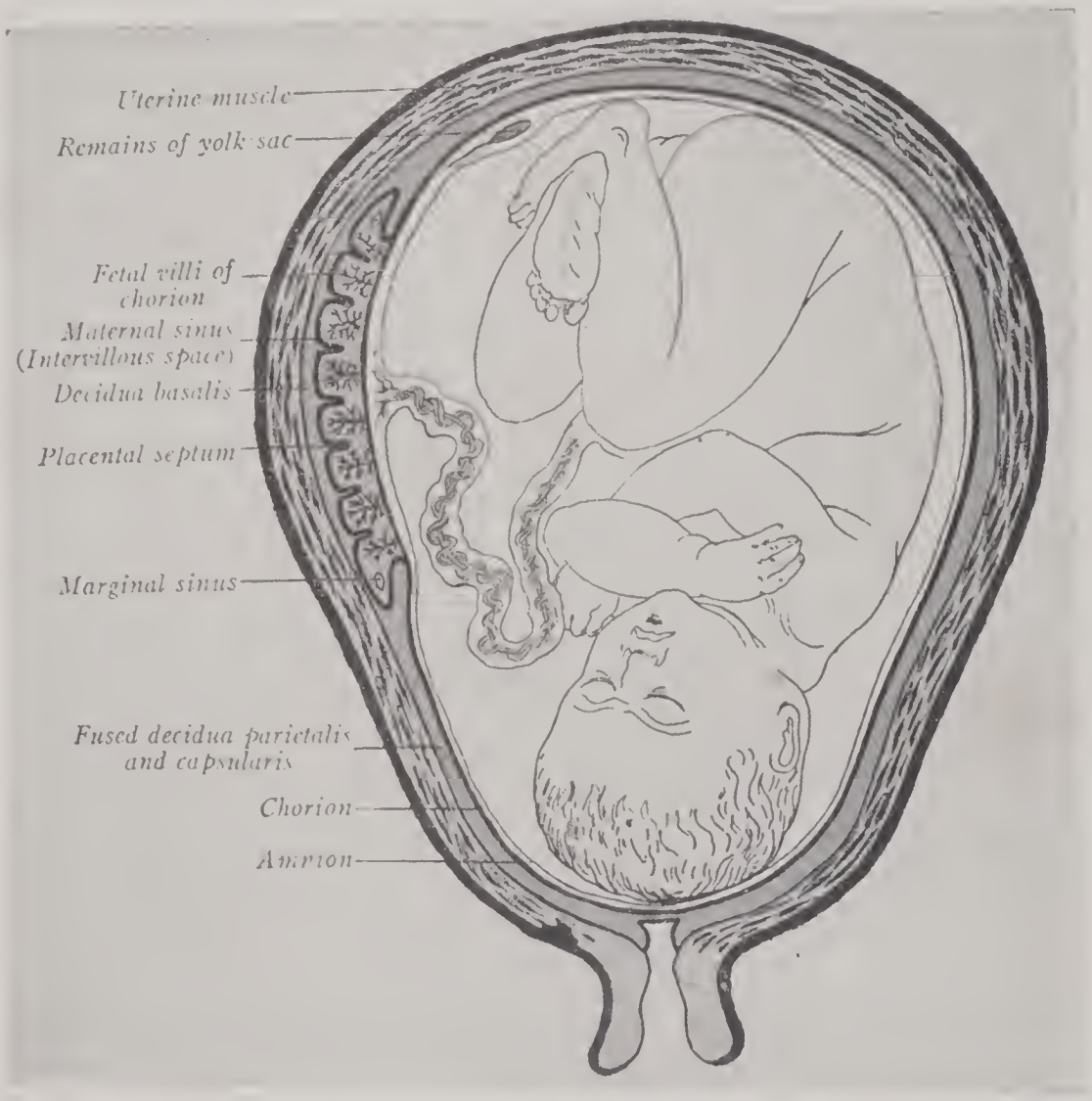


Fig. 181. Diagrammatic section through the uterus, showing the fetus shortly before birth. (Arey.)

five months, hair appears on the body and head. During the sixth month, eyebrows and eyelashes appear. After seven months the fetus resembles an old person with red and wrinkled skin. During the eighth and ninth months, fat is deposited under the skin, causing the wrinkles partially to smooth out; the limbs become rounded, the nails project at the finger tips, the original coat of hair is shed, and the fetus is "at full term," ready to be born (Fig. 181). The total **gestation period**, or time of development, for human beings is about 280 days from the beginning of the last menstrual period before conception, until the time of birth.

11. Formation of the Heart. In contrast to many organs which develop in the embryo without having to function at the same time, the

heart and circulatory system must function while still developing. The heart forms first as a simple tube from the fusion of two thin-walled tubes beneath the developing head. In this early condition it is essentially like a fish heart, consisting of four chambers arranged in a series: the **sinus venosus**, which receives blood from the veins; the single **auricle**; the single **ventricle**; and the **arterial cone**, which leads to the aortic arches.

In the beginning the heart is a fairly straight tube, with the auricle lying posterior to the ventricle; but since the tube grows faster than the points to which its front and rear ends are attached, it is forced to bulge out to one side (Fig. 182). The ventricle then twists in an S-shaped

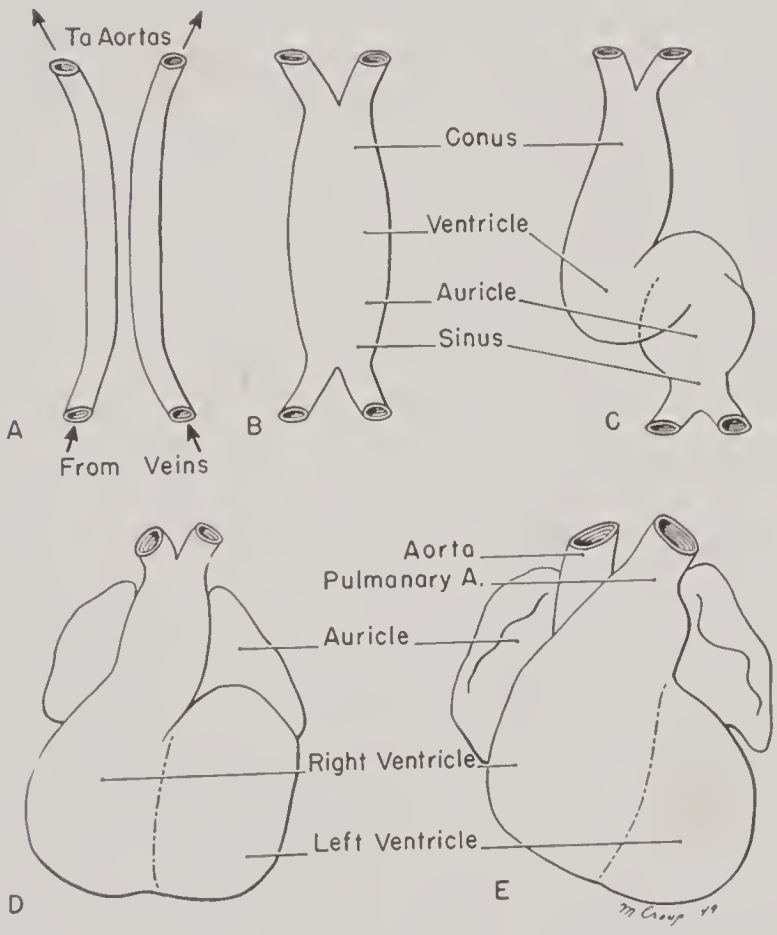


Fig. 182. Ventral views of successive stages in the development of the heart. See text for discussion.

curve down and in front of the auricle, coming to lie posterior and ventral to it as it does in the adult. The sinus venosus gradually becomes incorporated into the auricle as the latter grows around it, and most of the arterial cone is merged with the wall of the ventricle.

The embryonic heart, when it first appears, is a single structure with only one of each chamber, whereas the adult heart is a double pump, with separate right and left auricles and ventricles. This separation is necessary to prevent the mixing of aerated blood from the lungs with nonaerated blood from the rest of the body. Although the lungs are nonfunctional in the embryo, and not much blood passes through them, the heart begins separating into four chambers at an early stage. The two ventricles are completely separated by the end of the second month.

The auricles are partly separated, although complete separation does not occur until after birth, when the **oval window** between them finally closes. Before birth, this must be kept open to permit blood to get into the left side of the heart, for in the fetus only a small amount of blood passes through the lungs to the left auricle. Without this "window" the left side of the heart would be nearly empty, and most of the blood would pass through the right side only.

12. Development of the Digestive Tract. The digestive tract is first formed as a separate foregut and hindgut by the growth and folding of the body wall, which cut them off as two simple tubes from the original yolk sac. These tubes grow as the rest of the embryo grows, becoming greatly elongated. The lungs, liver and pancreas originate as hollow, tubular outgrowths from the original foregut, and hence are composed of entoderm. But these outgrowths always are associated with some mesodermal tissue, which forms the blood and lymph vessels, connective tissue and muscles of these organs. The entoderm forms only the internal epithelium of the digestive tract and lungs, and the actual secretory cells of the pancreas and liver. Both the enzyme-secreting cells and those of the islets of Langerhans in the pancreas are derived from the tubular outgrowths from the foregut. The lung first develops as a single median outgrowth from the ventral side of the foregut. This single tube, which is the forerunner of the trachea, soon branches into two, the rudiments of the bronchi, which in turn divide repeatedly and eventually grow into the complex structure which is the adult lung.

The most anterior part of the foregut flattens out to become, in cross section, a flattened oval, rather than a circle, and develops into the pharynx. In the pharyngeal region a series of five paired pouches, the gill pouches, bud out laterally from the entoderm and meet a corresponding set of inpocketings from the overlying ectoderm. In lower vertebrates such as fish, the two sets of pockets fuse to make a continuous passage from the pharynx to the outside—the **gill slits,** which function as respiratory organs.

In the higher vertebrates this normally does not occur; the pouches exist, but are nonfunctional vestiges which give rise to other structures or disappear. For example, the first pouch becomes the cavity of the middle ear and its connection with the pharynx, the eustachian tube. The second pouch becomes a pair of tonsils, while parts of the third and fourth pouches become the thymus gland, and other parts of them become the parathyroids. The fifth pouch is rudimentary and disappears. The thyroid develops from a separate outgrowth on the floor of the pharynx.

The mouth cavity arises as a shallow pocket of ectoderm which grows in to meet the anterior end of the foregut; the membrane between the two ruptures and disappears during the fifth week of development. Similarly, the anus is formed from an ectodermal pocket which grows in to meet the hindgut; the membrane separating these two disappears early in the third month of development.

13. The Development of the Kidney. With the general acceptance of the theory of evolution in the latter part of the nineteenth century, biologists were stimulated to study the development of a wide variety

of species to see how they resembled each other. These studies showed that the early development of all vertebrates is similar, and that, in general, those forms believed, from other evidence, to be most closely related have the most similar developmental processes. Moreover, it

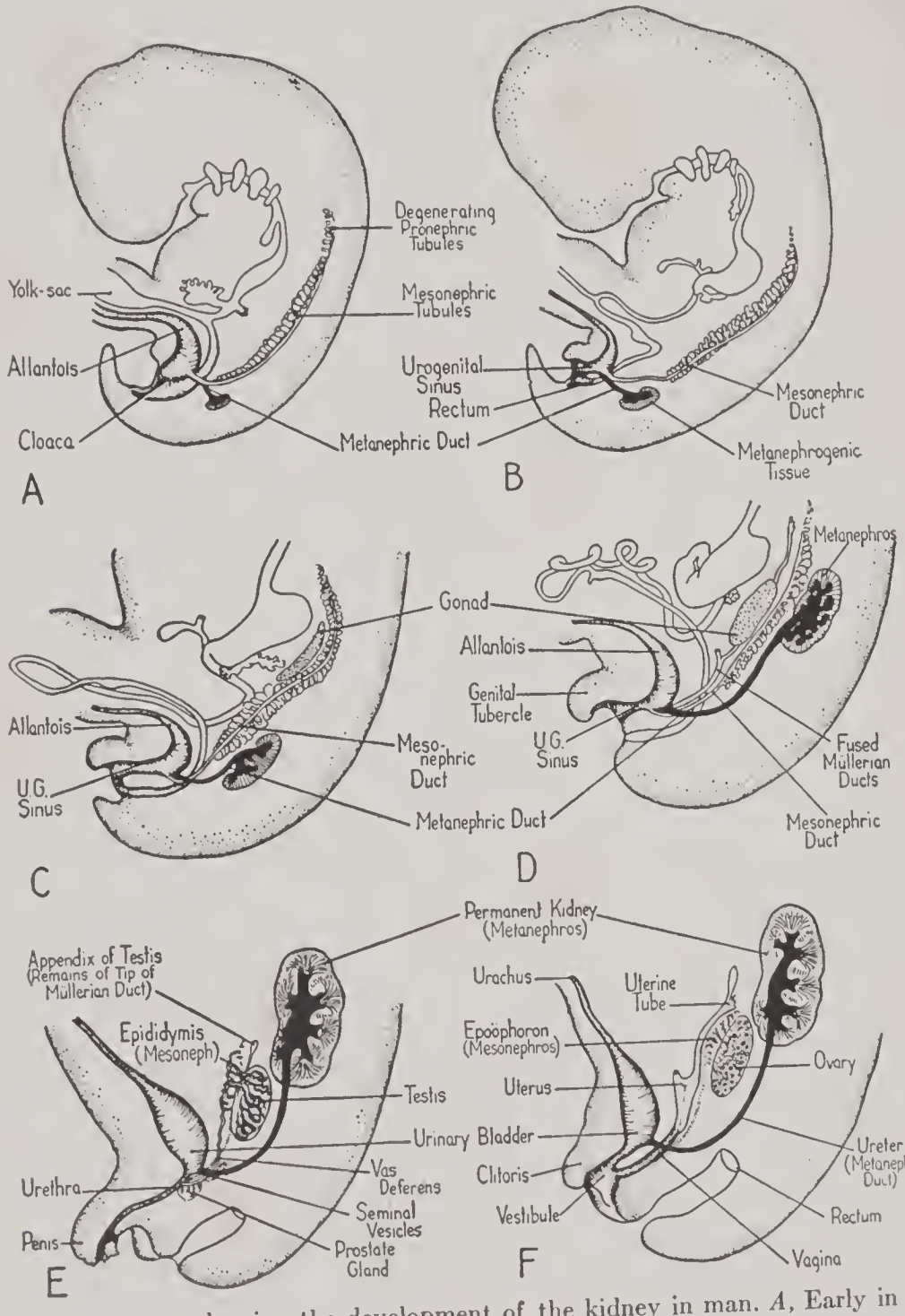


Fig. 183. Diagrams showing the development of the kidney in man. *A*, Early in the fifth week of development. *B*, Early in the sixth week. *C*, Seventh week. *D*, Eighth week. *E*, Three months (male). *F*, Three months (female). (Patten, B. M.: Human Embryology, The Blakiston Co.)

was found that the higher animals go through forms in development which resemble lower animals. From such observations arose the **theory of recapitulation.** This states that each individual in its embryonic growth recapitulates, or exhibits in structure, the steps in the evolution of its species. It has since been shown that the individual does not go through the adult stage of any of its ancestors, but repeats only the *embryonic* stages of those predecessors. Thus the human embryo devel-

ops gill pouches, like the fish embryo, but these never become gill slits, as they do in the adult fish.

The development of the kidney is one of the finest and most clear-cut examples of the principle of recapitulation. Within the class of vertebrates are three different types of kidney. The earliest—the fish kidney—called the **pronephros,** is the adult kidney of certain primitive fishes. The second, or **mesonephros,** is the adult kidney of amphibians and the higher fishes. The third, the **metanephros,** is the adult kidney of reptiles, birds and mammals. But in development, each of the higher animals repeats the evolutionary sequence of this organ. Thus frog embryos first develop a fish kidney, which functions during early embryonic life, before developing the permanent frog kidney. And man develops first a nonfunctional fish kidney, then a frog kidney, which may be functional during fetal life, and finally the permanent, third kidney or metanephros (Fig. 183). The three kidneys develop one after another in both time and space, each new kidney lying posterior to the previous one.

The pronephros, which in the human embryo consists of about seven pairs of rudimentary kidney tubules, develops in the mesoderm and degenerates during the fourth week of embryonic life. From the tubules a pair of ducts grows back to the hindgut and connects with it.

The tubules of the mesonephros originate during the fourth week, reach their heights at the end of the seventh week, and degenerate by the sixteenth week. These tubules connect with the ducts left by the degenerated pronephros, and empty into them. In the female the frog kidney and its ducts degenerate completely except for a few nonfunctional remnants, but in the male some of the tubules remain and are converted into the epididymides, while the ducts become the vas deferens.

The final kidney of reptiles, birds and mammals develops as a pair of buds from the ducts of the frog kidney. Or rather, the ureter and collecting tubules of the kidney develop from these buds, while the Bowman's capsules and convoluted tubules develop from the same sort of mesoderm that formed the tubules of the pronephros and mesonephros at a more anterior point. Later, these two portions unite to form the kidney tubules of the adult. The metanephros begins forming during the fifth week and is practically complete by sixteen weeks.

14. The Contributions of Each Germ Layer. The contributions of each of the three germ layers to the developing animal are summarized in the following table.

Ectoderm	*Entoderm*	*Mesoderm*
Epidermis of the skin	Lining of gut	Muscles—smooth, skeletal and cardiac
Hair and nails	Lining of trachea, bronchi and lungs	Dermis of skin
Sweat glands	Liver	Connective tissue, bone and cartilage
Entire nervous system: brain, spinal cord, ganglia, nerves	Pancreas	Dentine of teeth
Receptor cells of sense organs	Lining of gallbladder	Blood and blood vessels
Lens of eye	Thyroid, parathyroid and thymus glands	Mesenteries
Lining of mouth, nostrils and anus	Urinary bladder	Kidneys
Enamel of teeth	Urethra lining	Testes and ovaries

15. Control of Development. One of the most interesting problems in modern biology is to discover what kind of mechanisms cause development to proceed in a regular way, so that the organs appear at the proper time and in the proper relations to each other. Early embryologists, working with crude microscopes, thought that development was simply a matter of increasing size, that the germ of the adult was fully formed and differentiated with head, arms and legs, before growth began. One theory stated that this tiny creature was to be found in the egg, another that it was in the sperm, which simply had to enter an egg to begin growth. These **preformation** theories really explained development by denying that there was such a thing, and led to some amusing calculations. If all the individuals of one generation are contained within the eggs of their mothers, and these in turn are contained within the eggs of their mothers, and so on, like a series of Chinese boxes, then scientists seriously inquired, how many series of such boxes within boxes could have been accommodated in the ovaries of Eve, and how soon would those eggs be used up and the human race end?

With the development of better microscopes, it became apparent that there were no little people inside either sperm or eggs. It now is well established that each individual originates, as we have seen, from a single egg fertilized by a single sperm, and that development occurs by cell division and the progressive differentiation of these cells. This view is known as **epigenesis.**

But recently, with the development of experimental methods of study, investigators have found that development is not *simply* epigenetic. There are, it seems, certain *potentialities*, though not structures, localized in certain regions of the early embryo, and even of some eggs. When experimentally separated at the two-cell stage or even the four-cell stage, the embryos of some species continue to develop normally, indicating that each of the separated cells has the power to form an embryo complete in all details, although they are smaller than normal. Embryos of other species separated at the two-cell stage, however, demonstrate that certain potentialities are localized, for neither cell can develop into a whole embryo. Each half develops only those structures it normally would have—half an embryo, perhaps, or some part of one. This localization of potentialities *eventually* occurs in the development of *all* eggs; it simply occurs earlier in some than in others. From this we can deduce that some sort of chemical or physiological differentiation is present before any structural differentiation is visible, but the basic problem of how the chemical or physiological differentiation occurs remains unsolved. By a series of experiments it has been possible to map out the location of these potentialities in the primitive streak stage of the chick. Presumably, the potentialities in the human embryo at the comparable stage are similarly placed.

16. Organizers. An indication of how the differentiation mechanism may operate is provided by the experimental work of Spemann in Germany and of Harrison and Warren Lewis in this country. These investigators cut out, with tiny surgical tools, a bit of the upper lip of the blastopore of a frog or salamander gastrula, and implanted it beneath the ectoderm of another blastula. Here, the tissue healed in place, and

caused the development of a second embryo on the side of the host, resulting in a pair of Siamese twins. This blastopore lip region they named the **organizer,** because it organized the formation of the second embryo.

The ability to organize is widespread in developing tissues; many will organize the formation of an adjoining structure—the eyecup, for example, will initiate the formation of a lens from the overlying skin, even if it is transplanted to the belly region, where it must operate on cells normally destined to be belly skin. Development, then, is a coordinated series of chemical stimuli and responses, each step regularly following the previous step.

The term "organizer" is now applied not only to the organizing region, but to the chemical substance given off by that region, which diffuses to some other tissue and causes the latter to differentiate and develop in a particular way. Organizers are chemical entities, for they retain their organizing ability after being crushed, dried or boiled, and they may impart their inducing ability to some inert material such as gelatin or agar. But what their chemical composition is, is still a subject of inquiry.

Although organizers suggest a method whereby differentiation and development may be controlled, the entire problem is far from solved. Cleavage divisions occurring by the process of mitosis insure that each cell will get the same number and kind of genes as every other cell, and genes are believed ultimately to control development. Yet the cells resulting from the cleavage divisions are different from each other in their various developmental potentialities, possibly because of the interactions set up between like genes and dissimilar cytoplasms in the different cells.

17. Twinning. In man, apes and monkeys, as well as in many other species of mammals, a single offspring usually is produced at one time, although in other animals, more than one (up to twenty-five in the pig) are produced in a single litter. But about once in every eighty-eight human births, two individuals are delivered at the same time (twins). More rarely, three, four, five, and even six children are born simultaneously. These multiple births all belong to one of two types, due to two basically different situations. About three-fourths of the twins (and quadruplets, quintuplets, and so on) are the result of the simultaneous release of two eggs, one from each ovary, both of which are fertilized and develop. Such **fraternal twins** may be of the same or different sexes, and have only the same degree of family resemblance that brothers and sisters born at different times have, for they are entirely independent individuals with different hereditary characteristics. In contrast, **identical twins** (or triplets, and so on) are formed from a *single* fertilized egg which at some early stage of development divided into two (or more) independent parts, each of which develops into a separate fetus. Such twins, of course, are the same sex, have identical hereditary traits, and are so similar that it is difficult to tell them apart.

Occasionally, identical twins are not separated completely, but are born joined together and are known as **Siamese twins.** All grades of union have been known to occur, from almost complete separation, to

fusion throughout most of the body, so that only the head or the legs are double. Siamese twins always have separate brains, the separateness of their other organs depending on how intimately they are united. One twin may become sick independently and even die before the other, but the second will die within a few hours unless he is separated surgically from his twin. Sometimes the two twins are of different sizes and degrees of development, one being quite normal, while the second is only a partially formed parasite on the first. Such errors of development usually die during or shortly after birth.

Other malformations, such as a cleft palate, harelip or the formation of extra fingers or toes, are the result of irregularities in the developmental processes during the early weeks of development, and occur about once in every 165 births. The incidence is still higher in aborted fetuses.

According to popular superstition, such abnormalities are caused by fright or injury to the mother, and it is even supposed that injury to a particular part of the mother's body results in the malformation of that part of the fetus. Similarly, the benefits of listening to music, reading or thinking pleasant thoughts during pregnancy, are believed to be transferrable to the offspring as musical or literary abilities. Such superstitions have no basis in fact, for there is no connection whatsoever between the nervous systems of mother and child; moreover, injuries believed to cause malformations usually occur late in pregnancy, when the organs are already formed, and have been so since the second month of pregnancy.

Malformations may actually be due to any one of several causes: some have a hereditary basis; some are due to chemicals or toxins transferred from the mother's blood to the child's (by diffusion across the placenta); massive doses of X-rays or other penetrating rays cause others; and still others are caused by disease—such as German measles or syphilis—transmitted from mother to child via the placenta. In a great many cases the cause remains unknown, and is probably due to an accident of development.

18. The Changes at Birth. Great changes take place within a short time after a child is born. Hitherto it has received both food and oxygen from the placenta, now its own digestive and respiratory systems must function. Correlated with these changes are major changes in the circulatory system: the umbilical arteries and veins are cut off, and the blood flow through the heart and lungs is altered.

It is believed that the first breath of the newborn infant is initiated by the accumulation of carbon dioxide in the blood after the umbilical cord is cut, which stimulates the respiratory center in the medulla (see p. 184). The resulting expansion of the lungs enlarges the blood vessels therein, which previously were partially collapsed, and blood from the right ventricle thus flows in ever increasing amounts through the lung vessels, instead of through the arterial duct which connected the pulmonary artery and aorta during fetal life. The resulting increase in blood returning from the lungs to the left auricle results in the closing of the valvelike opening of the oval window (Fig. 184). These changes take place within a short period after birth, and eventually the flap of the

oval window grows into place and the arterial duct degenerates, so that the adult type of circulation is established. Occasionally the oval window fails to close or the arterial duct fails to degenerate, and there is a mixing of oxygenated and nonoxygenated blood which results in a "blue baby," a child whose skin has a purplish hue because of the inadequate oxygenation of its blood.

Development does not cease at birth, of course. At that time, such structures as the teeth and genital organs are only partly formed and

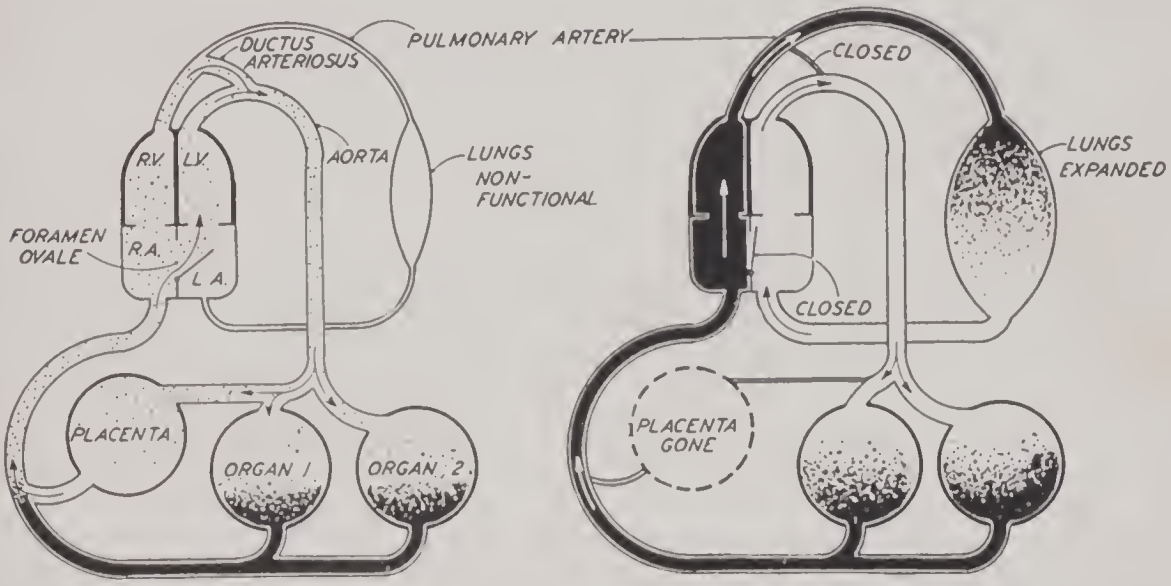


Fig. 184. Changes in the circulatory system at birth. The embryonic circulatory system is shown at the left; that of the newborn child on the right. Aerated blood is shown in white, nonaerated blood in black, and a mixture of the two is stippled. Note that in the embryo little of the blood goes through the lungs; most of the blood entering the right auricle gets into the aorta either via the oval window (*foramen ovale*) between the right and left auricles, or via the arterial duct (*ductus arteriosus*) between the pulmonary artery and aorta. The changes at birth are: (1) the absence of the placenta, (2) the expansion of the lungs, (3) the closing of the *foramen ovale*, and (4) the degeneration and closing of the arterial duct. (Carlson and Johnson: The Machinery of the Body, 3rd Ed., published by University of Chicago Press.)

the body proportions are quite different from those of the adult. The head, proportionally much larger than the rest of the body in early development, makes up about half the length of the two-month fetus, but its growth terminates in early childhood, so that the adult head is proportionately smaller than that of the newborn. The arms attain their proportionate size shortly after birth, but the legs attain their proportionate size only at the end of about ten years. The last organs to mature are the genitals, which do not begin to grow rapidly until between twelve and fourteen years after the infant is born.

QUESTIONS

1. What is the difference between isolecithal and telolecithal eggs?
2. What parts of the body develop from the ectoderm? the mesoderm? the entoderm?
3. What is the primitive streak?
4. What becomes of the notochord in the vertebrates?
5. How is the spinal cord formed?
6. What becomes of the gill pouches in the human embryo?
7. Trace the development of the kidney in the human embryo.
8. What is an "organizer?" How does it control development?

9. Differentiate between fraternal and identical twins. What are Siamese twins?
10. What causes a "blue" baby?
11. Describe sequence of events from fertilization to completion of neurulation in the frog.

SUPPLEMENTARY READINGS

Arey, L. B.: *Developmental Anatomy*. 5th ed. Philadelphia, W. B. Saunders Company, 1946.
A detailed discussion of human development; one of the standard texts.

Corner, G. W.: *Ourselves Unborn*. New Haven, Yale University Press, 1944.
An interesting, elementary presentation of embryology.

Patten, B. M.: *Human Embryology*. Philadelphia, The Blakiston Company, 1946.
An advanced but understandable discussion of human development.

Rugh, R.: *Experimental Embryology*. New York, John Wiley & Sons, Inc., 1949.
A clear, readable discussion, on an advanced level, of the results of experiments on the nature and controlling factors in development.

Weiss, P.: *Principles of Development*. New York, Henry Holt & Company, Inc., 1939.
A presentation of experimental embryology and a discussion of some of the factors controlling development.

PART V

MICRO-ORGANISMS AND INFECTIOUS DISEASES

CHAPTER 22

MICRO-ORGANISMS AND INFECTIOUS DISEASES

MICRO-ORGANISMS, as the name implies, are living things so tiny that they can be seen only through a microscope.* Some of them, such as the protozoa, resemble animals and are classified with them; others, the **bacteria,** are more similar to plants and are classified with them. In addition, other forms, called **filterable viruses,** have been known for many years, although they had never been seen before the invention of the electron microscope about 1935. This instrument, which

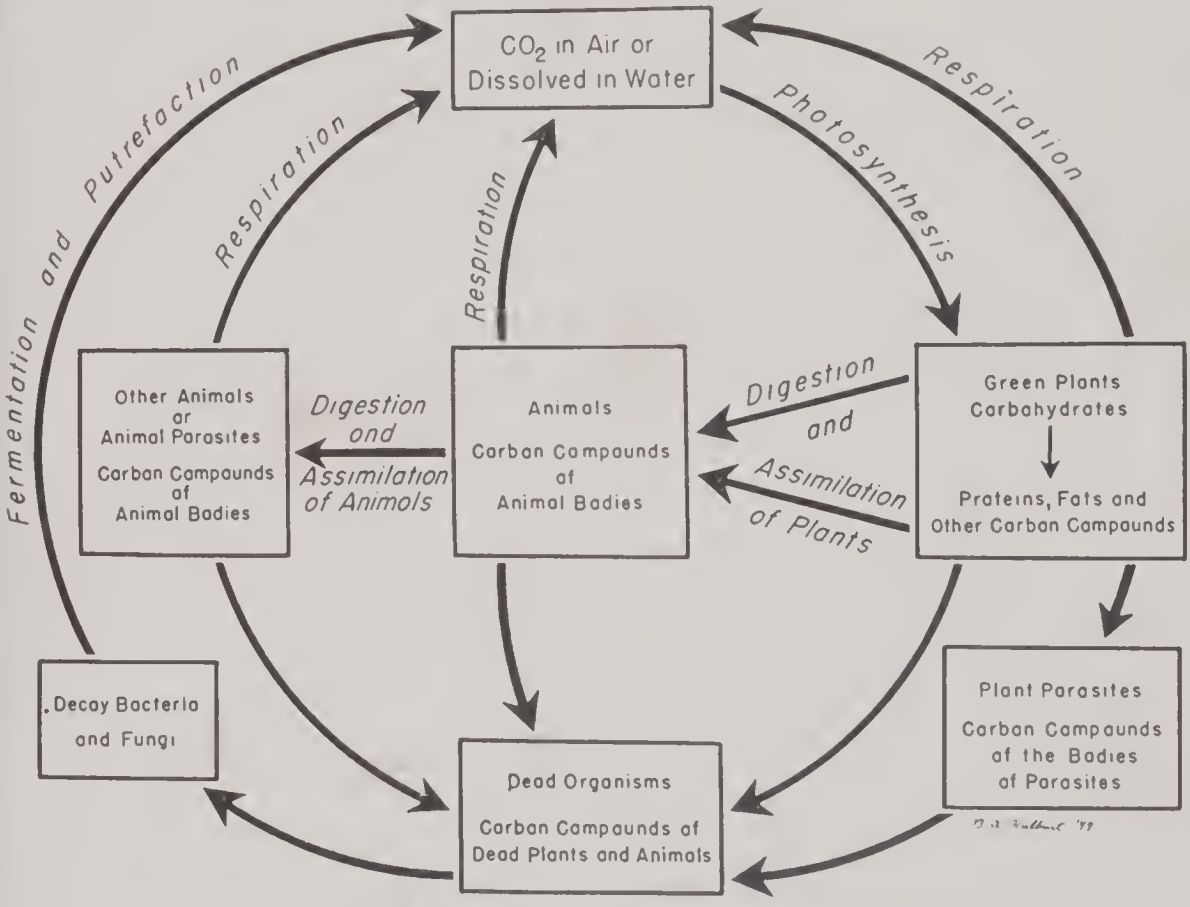


Fig. 185. The carbon cycle in nature. See text for discussion.

uses a beam of electrons instead of a beam of light, has extended the range of visibility to objects as small as 0.005 microns.

I. BACTERIA

For most people the words "disease" and "bacteria" are associated to such an extent that they cannot hear one without thinking of the

* What we can see through a microscope is limited by the wavelength of light, for if a particle is less than about half that wavelength, it will not interfere with the passage of light and hence not cast a shadow. By using light of extremely short wavelength—blue or ultra-violet—the limit of visibility for this instrument was established at about 0.2 micron.

other, but as we have seen already, many diseases are not caused by bacteria, and it is also true that *most bacteria do not cause disease.* The pathogenic types are only a small fraction of the thousands of kinds in existence.

1. The Carbon Cycle. Man and all other living things are dependent upon the majority of bacteria, for these tiny plants are necessary for decay, and hence for the fertility of the soil. In the endless cycle of matter, which is constantly taking place all over the earth, decay is essential

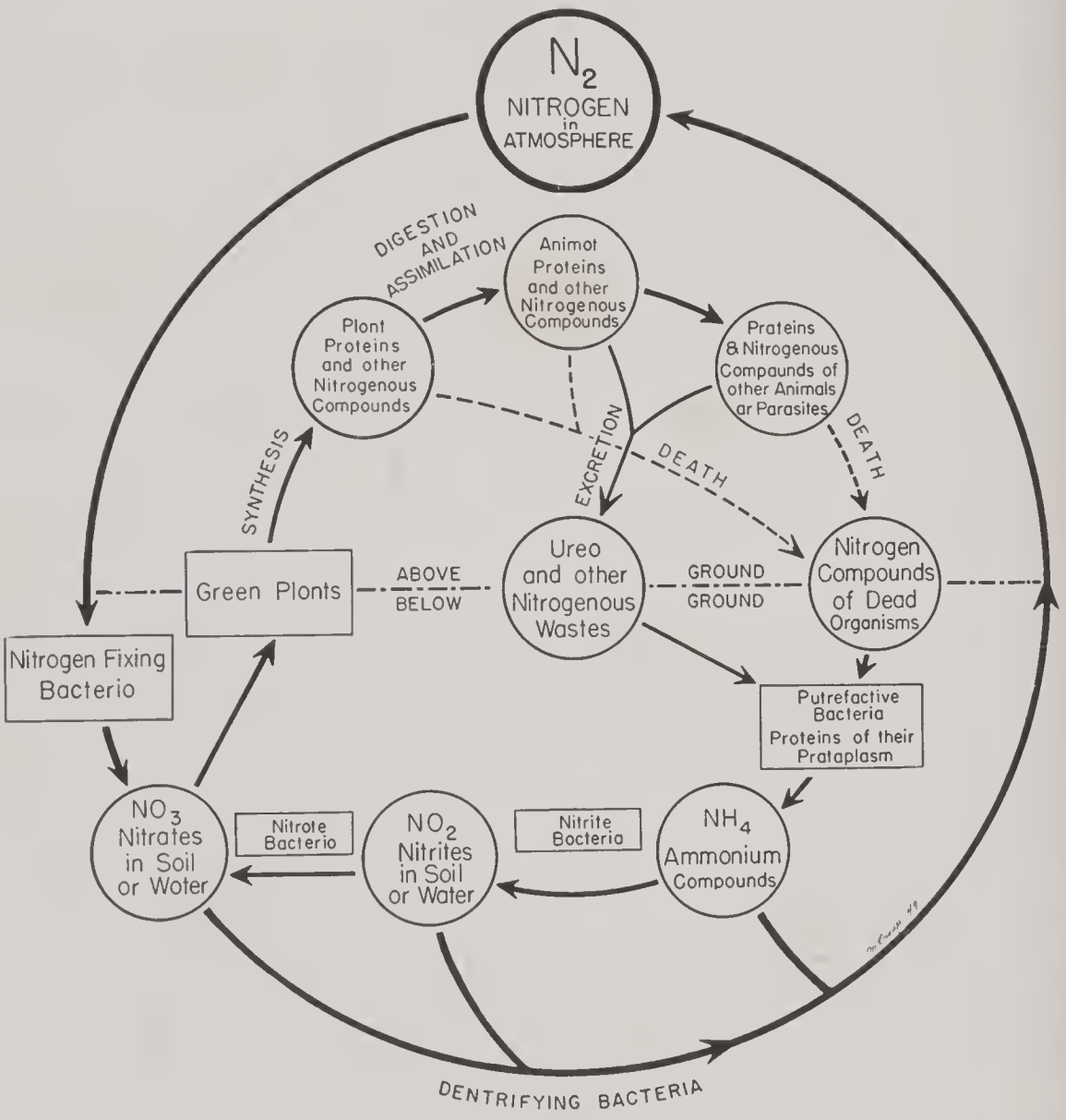


Fig. 186. The nitrogen cycle in nature. See text for discussion.

for returning to general circulation the basic chemicals (such as carbon and nitrogen) contained in the bodies of dead plants and animals (Fig. 185). Calculations show that there are about six tons of carbon (as carbon dioxide) in the atmosphere over each acre of the earth's surface. Yet each year an acre of plants, such as sugar cane, will extract as much as twenty tons of carbon from the atmosphere for incorporation into the plant bodies. Thus at the average rate of consumption of carbon dioxide, the plants would use up all the atmospheric supply of this substance within thirty-five years. But decay bacteria perform the function of breaking down chemically the complex, organic compounds of the dead

matter of the earth to simple, inorganic substances and so make them available for use by new life forms.

2. The Nitrogen Cycle. Nitrogen too is freed from dead material by bacteria. The source of all nitrogen essential for the synthesis of amino acids and proteins—hence for all protoplasm—is the nitrates in the soil (Fig. 186). These nitrates are absorbed by plants and synthesized into the amino acids and proteins of plant protoplasm. The plants are then eaten by animals that in turn use them for synthesizing their protoplasm. When the animals and plants die, the decay bacteria convert the nitrogen compounds into ammonia, and "**denitrifying**" bacteria convert some of the ammonia into atmospheric nitrogen. The rest of the ammonia is used by other kinds of bacteria as a source of energy, and, in the process, the ammonia is converted into nitrites. Hence these bacteria are known as **nitrite** bacteria. Finally, other (**nitrate**) bacteria convert the nitrites to nitrates, thus returning the element to the soil and completing the cycle. The atmospheric nitrogen is converted to nitrates by still other ("**nitrogen-fixing**") bacteria which live in the soil at the roots of leguminous plants. This is fortunate, for, in spite of the fact that almost 80 per cent of the atmosphere is nitrogen, no animals and only a few plants can utilize it in that form. Today, some nitrates are made artificially and added as fertilizer to the soil, but the action of bacteria is still absolutely essential; without it, life would cease for lack of raw materials.

3. Bacteria in Industrial Processes. Bacteria are responsible for many other processes of particular value to man. Some bacteria are used commercially to produce acetone and butyl alcohol, widely used as solvents. Others, by digesting the covering of seeds, are important in the production of coffee and cocoa. Bacterial action is necessary for curing raw tobacco leaves, and for manufacturing linen and rope from flax and hemp. The latter plants are held together by a gum called pectin, which the bacteria digest, thus freeing the fibers so they can be spun into thread or woven into rope. Other substances whose production involves the use of bacteria are butter, cheese, sauerkraut, rubber, cotton and silk, to mention just a few.

4. Types of Bacteria. Although they do not contain chlorophyll, bacteria are usually classified as plants.* They consist of one cell only (usually surrounded by a slimy capsule), which in some types has a distinct nucleus (Fig. 187), but in others contains nuclear material in the form of scattered, granular bits. The entire cell is about $\frac{1}{20,000}$ inch long. Like all living things, bacteria utilize energy by oxidizing food materials; both food and gases penetrate the cell membrane by diffusion.

Some bacteria use oxygen from the air or from the surrounding liquid and are called **aerobic;** others, called **anaerobic,** are able to obtain their oxygen supply by breaking down organic compounds which contain it, and some of these cannot live in the atmosphere.

Bacteria can move only in fluids and cannot leave a fluid by their own efforts, but by becoming attached to a dust particle or water droplet they travel considerable distances through the air. To facilitate move-

* In the phylum Thallophyta, which includes fungi and algae. Some investigators put bacteria in a separate phylum within the plant kingdom, but usually they are classified as one group of the subphylum Fungi, of the phylum Thallophyta.

ment, many of them have whiplike projections—cilia or flagella—which act as propellors. Many bacteria are capable of changing into spores, those tough, resistant forms, difficult to kill, which tide many plants over periods when the environment is unfavorable—perhaps too hot, too cold or too dry. Fortunately, most disease-causing varieties do not form spores.

Bacteria exist everywhere: in the air, in fresh and salt water, in the soil, frozen in ice, and in the bodies of plants and animals. Because of

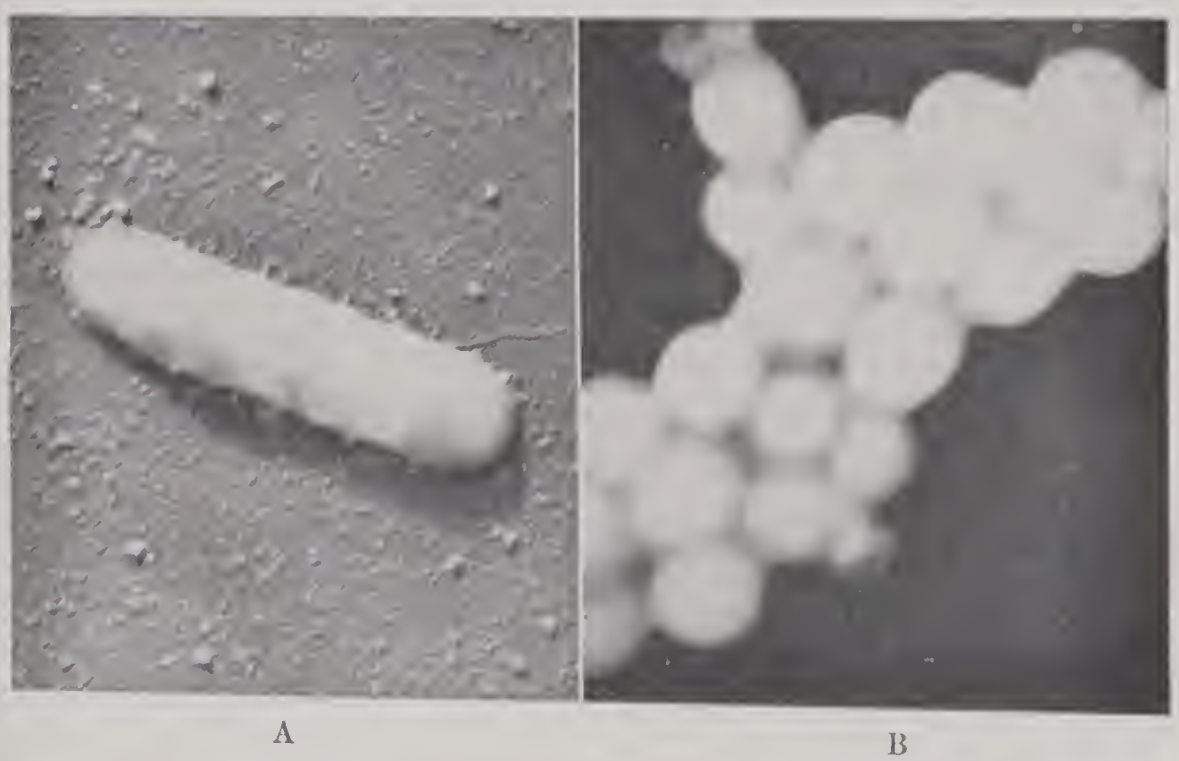
Fig. 187. The dark-staining bodies of *Bacterium coli*, which are believed to represent the nucleus. Successive stages in the development of a single, oval-shaped cell with a broad, central nucleus or chromosome (*a*) into a long, rod-shaped, two-celled bacterium with two pairs of chromosomes (*h*). In *e*, a fine strand of nuclear material can be seen connecting the two recently divided chromosomes. (Robinow, C. F. in Cambridge J. Hygiene, Vol. 43.)

their small size and general similarity of structure, they are usually classified more on the basis of their physiological and biochemical characteristics than on morphological differentiations. But most of them do exhibit one of three shapes. There are rodlike forms called **bacilli**, spherical forms called **cocci**, and spiral forms (Fig. 188). The bacilli may occur as single rods (Fig. 189) or, as in the bacillus causing anthrax, as long chains of rods joined together. Diphtheria, typhoid fever, tuberculosis and leprosy are all caused by bacilli. The spherical forms occur

singly in some species; in groups of two (as the pneumococcus, causing pneumonia); in groups of four (as the gonococcus, causing gonorrhea); in long chains (as streptococci and the bacteria causing scarlet fever);

Fig. 188. Types of bacteria. *A–E*, Spherical bacteria or cocci. *F*, Coccobacilli, intermediate between cocci and bacilli. *G–I*, Rod-shaped bacteria or bacilli. *J*, Curved rods. *K* and *L*, Spiral forms. (Burrows, W.: Jordan-Burrows Textbook of Bacteriology.)

or in irregular clumps, resembling bunches of grapes (as the staphylococci which cause boils, Fig. 189). There are two types of spiral forms: the spirilla, which are less coiled and sometimes resemble a comma (the



A B

Fig. 189. Photographs made with an electron microscope of bacteria which were shadowed with gold to demonstrate depth. *A*, Single, rod-shaped bacillus; *B*, A group of staphylococci—spherical bacteria which occur in bunches like grapes. (Burrows, W.: Jordan-Burrows Textbook of Bacteriololgy.)

one causing cholera is like this); and the spirochetes, which are highly coiled like a corkscrew. The most widely known of the latter is that causing syphilis.

5. Reproduction of Bacteria. Bacteria reproduce by simple fission—the division of one cell into two. It has been found recently that many, and perhaps all of them, divide by a process resembling mitosis. They do this with remarkable speed, some bacteria dividing once every twenty minutes. At this rate, if there were plenty of food and nothing to interfere, one bacterium could give rise to about 500,000 bacteria within six hours. After twenty-four hours the resulting mass would weigh 4,000,000 pounds, and in less than a week this single bacterium could give rise to a mass of bacteria the size of the earth!

6. Bacterial Metabolism. Like other organisms, bacteria secrete enzymes, some of which act within the cell, while others pass to the outside and cause chemical reactions in the surrounding matter, such as those mentioned in connection with the carbon and nitrogen cycles. When the surrounding material happens to be a carbohydrate, such as sugar, starch or cellulose, the chemical breakdown process is called **fermentation.** Some bacteria break carbohydrates down to carbon dioxide; others stop at intermediate points. For example, the bacteria which sour milk break the milk sugar down to lactic acid, and other bacteria convert the alcohol of wine or cider to the acetic acid of vinegar. When the medium in which the bacteria live is protein, the decomposition carried on by their enzyme action is called **putrefaction.** The foul smells associated with the decay of food and bodies are due to the nitrogen and sulfur-containing compounds which result from these breakdowns. Another type of enzyme action results in the breakdown of fats to glycerine and fatty acids.

II. OTHER MICRO-ORGANISMS

Much smaller than bacteria, indeed scarcely larger than very large molecules, are other forms, called **viruses, bacteriophages** and **rickettsias.** With the exception of the last, these are too small to be seen with ordinary microscopes, and can be photographed only with the aid of the electron microscope. None of them is classified as either plants or animals, and their status in the world of living things is still not definitely understood. Some investigators believe that they are not living organisms at all, but large protein molecules which simulate some of the characteristics of life, such as independent movement and reproduction. In the following discussion, then, we shall use the word "organism" for convenience and with certain reservations.

7. Filterable Viruses. These ultramicroscopic forms, which take their name from the fact that they are tiny enough to pass through very fine-pored, porcelain filters, were first demonstrated to exist by Iwanowski in 1892, when he showed that a disease of tobacco plants (tobacco mosaic) could be transmitted to healthy plants by the sap of diseased ones, even after it had passed through filters fine enough to remove all bacteria. Today, many diseases of both plants and animals are known to be caused by viruses; a few economically important ones are hog cholera, swine influenza, chicken cancer and the foot-and-mouth disease which has plagued the cattle herds of Mexico and Argentina (Fig. 190). The list of virus diseases of man includes smallpox, rabies, infantile paralysis, measles, yellow fever, warts, fever blisters and the common cold.

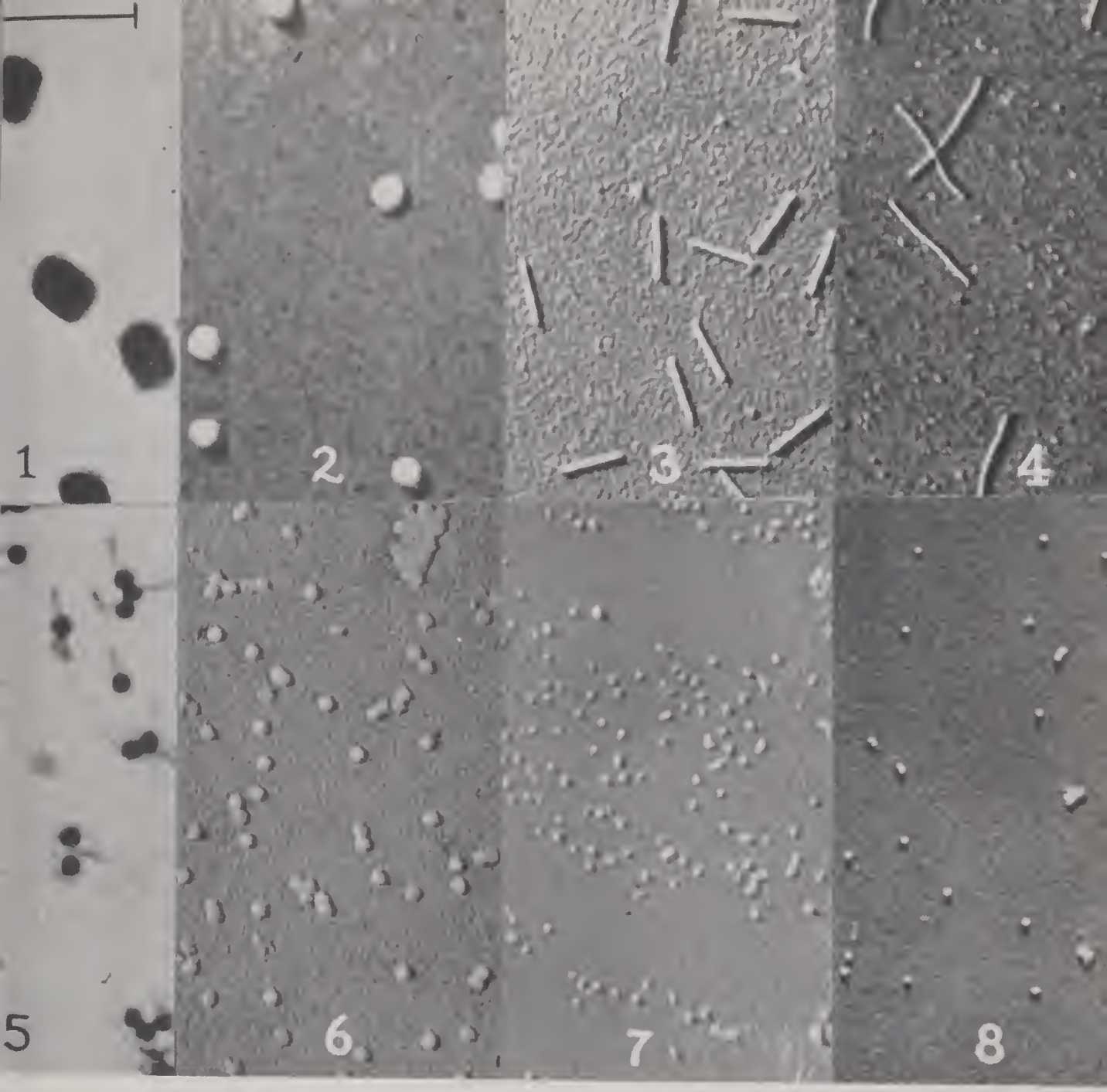


Fig. 190. Photographs made with an electron microscope of a variety of viruses, *1*, Vaccinia virus (used in vaccinating for smallpox). *2*, Influenza virus. *3*, Tobacco mosaic virus. *4*, Potato mosaic virus. *5*, Bacteriophages. *6*, Shope papilloma virus. *7*, Southern bean mosaic virus. *8*, Tomato bushy stunt virus. Numbers 2, 3, 4, 6, 7 and 8 were shadowed with gold before being photographed in the electron microscope. (Courtesy of Dr. C. A. Knight.)

Fig. 191. Photograph made with an electron microscope of bacteriophages (the small bodies shaped like a ping-pong paddle) attacking bacilli (the large, sausage-shaped structures). Magnification about 17,000 times. (Burrows, W.: Jordan-Burrows, Textbook of Bacteriology; photographs by Auria and Anderson.)

A vast amount of research has been done to determine whether human cancer is caused by viruses, but at present there is no evidence that it is. One type of breast cancer in mice has been found to be caused by a virus-like agent, but human cancers are not infectious, as a virus disease should be.

Viruses can easily be grown in an artificial medium containing other living cells, and apparently they can reproduce *only* in such an environment; this has given rise to the opinion that they do not really reproduce, but are reproduced *by* other living cells. A common virus medium consists of the cells of a chick embryo, minced in a nutrient salt solution; many viruses which will not grow if injected into a living chicken thrive on this medium.

Estimates of the size of viruses have been made in a number of different ways: from the size of the filter pores which permit them to pass, from the speed with which they settle when centrifuged, and from measurements of electron microscope photographs of them. These measurements show that viruses vary widely in size; one of the largest—the vaccinia virus, used in vaccinating against smallpox—is about 200 millimicrons in diameter,* and one of the smallest—that of infantile paralysis—is 15 millimicrons in diameter. The electron microscope shows some viruses to be spherical, others to be rod-shaped (Fig. 190).

Viruses usually attack specific parts of the body: those of smallpox, measles and warts attack the skin; those of infantile paralysis and rabies attack the brain and spinal cord; and those of yellow fever attack the liver. Fortunately, infections caused by viruses create lasting immunity against them, and inoculations for smallpox, rabies and yellow fever are highly successful.

8. Bacteriophages. Some of the most interesting types of viruses, called **bacteriophages** ("phage" means eater), are parasites of bacteria only. They were discovered by a French scientist, d'Herelle, when he observed that some lethal agent was present in his bacteria cultures. Like other viruses, bacteriophages are filterable, and will grow only in the presence of living cells—specifically, in cultures of bacteria, which they cause to swell and dissolve. These viruses usually occur in nature wherever bacteria are found and are especially abundant in the intestines of man and other animals.

There are different varieties of bacteriophages, each of which attacks a particular kind of bacteria. Electron microscope photographs (Fig. 191) show that some are about 5 millimicrons in diameter (they vary considerably in size), and that many of them are spherical, while others have short tails and are comma-shaped. The fact that bacteriophages can destroy bacteria suggests, of course, that they be used to combat bacterial diseases, and many bacteriophage preparations have been given, without much effect, to patients suffering from such diseases as dysentery and staphylococcus infections. Such experiences, as well as laboratory evidence, indicate that bacteriophages are ineffective in the presence of blood, pus or fecal material, and their use for therapeutic purposes has been practically abandoned.

* A millimicron is a thousandth of a micron, one twenty-five millionth of an inch.

To obtain bacteriophages in the laboratory, an emulsion of feces is made and passed through a fine filter. When a drop of the filtrate is added to a turbid bacterial culture, the bacteriophages kill and dissolve the bacteria, leaving the culture clear (Fig. 192). When this culture is filtered in turn and a drop of the new filtrate placed on a second bacterial culture, the latter also will clear. Thus, serial transfers of the bacteriophage can be made indefinitely, and since bacteriophages multi-

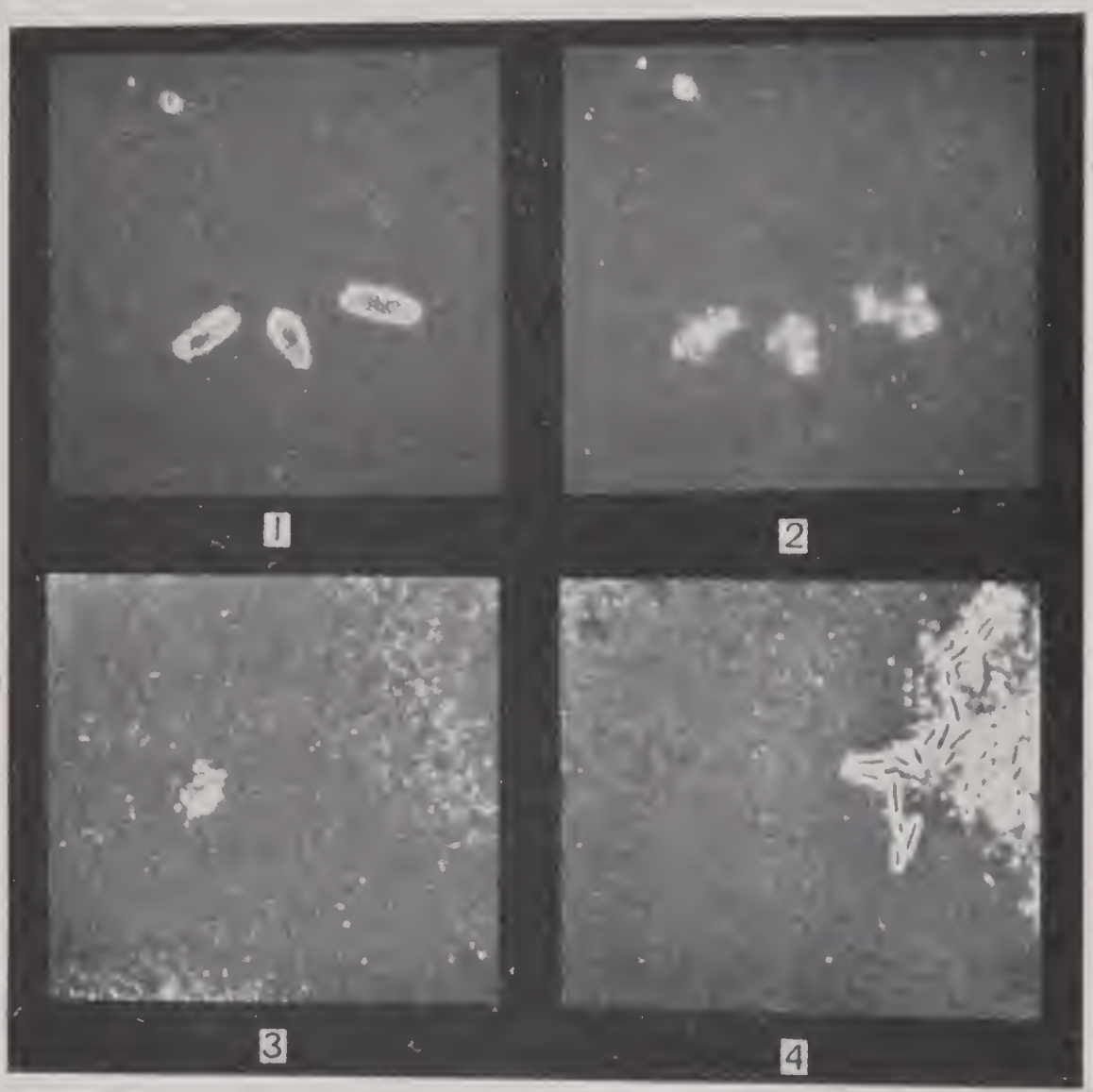


Fig. 192. Photographs of stages in the destruction of bacteria by bacteriophages. *1*, Three bacilli, showing the bacteriophage bodies inside the cells, three hours after they first entered. *2*, Five minutes later, the bacteria have collapsed and the bacteriophages have been released. *3*, Bacteriophages floating freely in the culture medium. *4*, Example of bacteria resistant to bacteriophages growing in the presence of free bacteriophages. (Merling-Eisenberg, in Burrows, W.: Jordan-Burrows, Textbook of Bacteriology.)

ply rapidly, each successive filtrate becomes more potent in killing bacteria.

9. Rickettsia. These disease organisms, named after their discoverer, Ricketts, who died of typhus while studying the rickettsia that causes it, seem to be on the borderline between viruses and bacteria. Barely visible under the microscope, they appear to be living and capable of changing form (Fig. 193). Some are spherical, others rod-shaped, and

they vary in length from 300 to 2000 millimicrons. Unlike viruses, they are microscopically visible and non-filterable, but most of them resemble viruses in failing to multiply outside living cells, although a few have been cultivated in special laboratory media. Rickettsias are found in the intestinal tracts and salivary glands of insects, such as lice, bedbugs and ticks, and are transmitted to man and other animals by the bites of these insects. The principal diseases in the United States caused by these organisms are typhus fever (not to be confused with typhoid fever, caused by a bacillus) and Rocky Mountain spotted fever.

10. Fungi. In the chapter on plants we discussed the place of fungi in the plant kingdom, as well as their general characteristics. Now we must reconsider them as disease agents, though not all types of fungi cause disease. The group is large and includes such diverse (and harmless) forms as mushrooms and slime molds.

It is not coincidental that the two forms of plants which cause disease —fungi and their relatives, bacteria—are distinctive in lacking chloro-

Fig. 193. An epithelial cell infected with rickettsias in the cytoplasm. Typical rickettsias are indicated by the arrows. (Frobisher, M., Jr.: Fundamentals of Bacteriology.)

phyll. For plants with chlorophyll are capable of making their own food and do not need to live parasitically. Many forms of fungi, while unable to live independently of other life forms, obtain their food from decaying organic matter,* but others with which we are concerned here, cannot do so and are constantly invading other plants and animals for nourishment.

Like other members of their class, pathogenic fungi are of various sizes; those attacking plants are usually large enough to be seen with the naked eye, while most of the ones attacking animals are microscopic. All are either multicellular or multinuclear.

The common human disease of ringworm or "athlete's foot" is not caused by a worm, but by any one of several species of fungi, which grow under the surface of the skin. They survive and obtain nourishment there by secreting enzymes which digest the tough, insoluble pro-

* They are thus important, like bacteria, in the carbon and nitrogen cycles. Bacteria, however, operate in moist places, while fungi carry on the processes of decay in drier environments.

tein (called keratin) of the skin's dead, outer layer. Only a few other organisms, notably the clothes moth and the carpet beetle, have similar enzymes for digesting this protein. Other, more serious, but much rarer diseases of man are the result of certain fungi becoming established in the internal organs, such as the liver or lungs. Rat-bite fever is one such fungous disease transmitted by the bite of an infected rat.

Much more detrimental to other plants than to animals, fungi cause enormous economic losses. They attack plants by entering through an opening such as a wound, and from there proceed on through or between the plant cells, forming a matted mass of threads. Downy mildews are fungous diseases attacking melons, grapes and potatoes, and Ireland's potato blight of the 1840's, which resulted in a famine that killed over 250,000 people and caused a mass migration to the United States, was the result of one of them. Some other fungous diseases of plants are peach-leaf curl, canker, the molds which rot fruits and vegetables, wheat rust, stinking wheat smut, wilts (which result when the matted growth of the fungi obstruct the xylem and phloem vessels, cutting off the supply of water), and bracket fungus rot (Fig. 194).

11. Protozoa. Of the thousands of species of protozoa, only about twenty-five are human parasites,* and hence agents of infectious diseases. These organisms, though microscopic, are not so small as bacteria, the pathogenic ones varying in diameter from 3 to 80 microns. Since the types of protozoa causing disease are not homogeneous, but represent all four classes of the phylum, it is difficult to generalize about their characteristics. All, of course, are single-celled, but in their internal structures, outer shapes, methods of locomotion and of reproduction, they vary greatly. The most important human diseases caused by them are malaria, African sleeping sickness, and amebic dysentery (see p. 407).

III. WORMS

We turn now from our discussion of micro-organisms to a consideration of some larger parasites. Several classes of worms have parasitic members: a majority of the flatworms are so, the best-known being lung flukes, blood flukes and tapeworms. While most of the round worms are free-living, a few are parasitic—those parasitizing man include the pinworm, whipworm, *Ascaris* and hookworm, all of which live in the intestine, and the trichina worm, which dwells in the muscles (see p. 409). In length, these worms vary from a millimeter or two to several meters, and hence are easily visible to the naked eye (macroscopic). Many of them have complex body structures and complicated life-cycles, and their stages of reproduction usually occur in two or more kinds of animals. Thus, although certain types spend their entire adult lives within the human organism, they do not multiply there, and once wiped out, can reappear only by reinfection.

IV. INSECTS

Insects, the last of the types of pathogenic organisms to be discussed, are also macroscopic, although they vary from tiny forms, such as aphids,

* There are many more species parasitic in plants and other animals, but most species are free-living.

to large ones such as wasps. Although man and other animals are infected by them, their chief victims are plants. Like the worms, they are so various—representative of so many different orders—that one cannot describe a "typical" parasitic insect. A few common ones are the scale insects, gall insects (wasps), and aphids, or plant lice. Scale insects burrow into plants and live by sucking their juices, but, paradoxically, they often secrete a poison which kills the host and necessitates their

Fig. 194. The trunk of a tree infected with a bracket fungus which produces the shelflike bulges. (After Schrenk and Spaulding: Journal of Agricultural Research; in Frobisher, M., Jr.: Fundamentals of Bacteriology.)

finding another one. Gall insects operate by laying eggs under the bark of a tree; when the larva hatches from the egg, it feeds on the tissues of the plant, stimulating them to grow a round ball (gall) around its body. The larva passes the winter in the center of this gall, and in the spring changes into an adult and bores its way out. Meanwhile, the tree often dies.

The San Jose scale, which invades apple, peach and plum trees, and

the cottony cushion scale, which attacks orange and lemon trees, are the most serious scale pests in America. One effective way of combating them is to import other insects which are their natural enemies, but spraying with various insecticides, notably DDT, is helpful and often more convenient.

Many insects which do not directly cause disease are detrimental to plants and animals in that they carry infectious micro-organisms.

V. ANTIBIOTICS

In any natural environment there are many species of bacteria and fungi, some of them antagonistic to others.* As early as 1879 it was known that, when micro-organisms are grown together in the laboratory, one usually overcomes and kills the others. This phenomenon was given the name "antibiosis" and was first explained as being due to the organisms' competition for the same nutrients. Investigators later realized that certain organisms manufacture substances which are detrimental and even lethal to others, and these they called **antibiotics.** The earliest antibiotic to be discovered (pyocanin) was isolated from pus in 1860, even before the bacterium which produced it was known. Many antibiotics have since been isolated from bacteria, and from a wide variety of plants, such as tomatoes and onions.

Unlike bacteriophages, antibiotic chemicals are successfully used against pathogenic bacteria. Today, the most important ones are isolated from molds. Of these, **penicillin,**† which comes from a fungus closely related to those of Roquefort and Camembert cheese, is the most efficacious. Actually, there are three different forms of this antibiotic, only one of which is highly active against bacteria. In contrast to many other antibiotics, it is not toxic when injected into man and other animals. Bacteria exposed to the action of penicillin swell and cannot divide, so that they are easily destroyed by the body's white blood cells.

Not all bacteria are vulnerable to penicillin, of course; some are susceptible to **streptomycin,** the second most widely used antibiotic, which is extracted from **actinomyces**—organisms intermediate between bacteria and fungi. Still other antibiotics—flavicidin, notatin, aspergillic acid, and so forth—come from various other fungi, but are not so useful as penicillin and streptomycin, because they are more toxic. The antibiotics are of diverse chemical natures: some are protein-like, some are fatlike, and some are complicated organic chemicals of other types. They are much more active against bacteria than the sulfa drugs, which they have almost completely replaced in the treatment of many diseases.

VI. THE GERM THEORY OF DISEASE

It is rather startling to think that a hundred years ago, man knew little more about the nature of contagious diseases than was known by the early Greeks. But through all the centuries of recurring plagues,

* Others are mutually dependent, a relationship called **symbiosis** (see p. 102).

† This was first discovered by Fleming in 1929, but its possibilities were not fully appreciated until 1940.

which swept countries and continents, killing thousands upon thousands of people, there was apparently no inkling of what caused and spread them. It was not until about 1870 that man first realized the significance of the micro-organisms which enter the body and either attack the tissues directly or produce toxins which do.

Louis Pasteur, a French scientist of the nineteenth century, has become an almost legendary figure as the man who first established the germ theory of disease. He made his discovery as the result of studying the "diseases" of souring wine and beer. These processes are caused, he found, by micro-organisms which enter the wine or beer from the air and bring about undesirable fermentations, which yield products other than alcohol. He found that by gently heating (a process now called **pasteurization**) the grape juice or beer mash to kill the undesirable organisms, he could prevent these "diseases." At the request of the French silk industry he studied a disease of silkworms, which proved to be caused by another micro-organism. From these facts Pasteur reasoned that many plant and animal diseases might be caused by similar germs invading the body, and he next investigated anthrax (a disease of sheep and cattle) and then chicken cholera. His treatment, inoculation, greatly reduced the death rate from these diseases and, needless to say, became standard practice. Later he invented the cure now used for rabies or hydrophobia, the disease contracted through the bite of a mad dog.

Lord Lister, an English surgeon, was one of the first to understand the significance of Pasteur's discoveries and to apply the germ theory to the procedures of surgical operations. He initiated antiseptic techniques by dipping all his operating instruments into carbolic acid and by spraying the scene of the operation with that germicide, thus effecting a marked decline in the number of fatalities following operations, which previously had been high even for minor ones.

After Pasteur, important contributions were made to the new science of bacteriology by the German physician Robert Koch, who went to great pains to prove absolutely that anthrax is caused by a particular organism. In so doing, he developed methods for isolating pure cultures of bacteria and for growing the cultures outside the body of the normal host. By extracting blood from an animal suffering from anthrax, and growing the bacteria from it in artificial cultures—transferring them from culture to culture many times—he eliminated the possibility that some contaminating chemical might have been causing the disease. Bacteria from the last culture, when injected into a new animal, produced anthrax: it could no longer be doubted that these organisms were the true cause of the disease.

12. Koch's Postulates. The evidence necessary to prove that a particular micro-organism is the cause of a disease is often condensed into a series of statements or postulates, commonly called Koch's postulates, because of his pioneer work in the field. They are a classic example of how the scientific method operates and are included here.

1. The micro-organisms must be observed in the blood or tissues of the infected animal, and must have a reasonable pathological relationship to the disease symptoms and lesions.

2. The organisms must be isolated from the diseased host and grown outside the body in a pure culture.

3. A portion of this culture must be injected into a second, noninfected animal, and the symptoms and lesions of the first animal must appear.

4. The organism must be observed in, and recovered from, the experimentally diseased animal in pure culture.

After the discoveries of Pasteur and Koch many investigators worked on the problem of isolating and describing micro-organisms, and we now have the benefit of their efforts in a large body of knowledge about infectious (or contagious) diseases—those ailments which are caused by the invasion of some organism, and which can be transmitted from one individual to another.

With the infectious diseases we complete our survey of the main types of disease, and now we can understand fully how they differ from those mentioned previously. To sum up, the word "disease" means any malfunctioning of a plant or animal body, and includes those caused by the lack of some nutrient (deficiency diseases), those caused by some abnormal functioning of the cells, such as cancer or the endocrine diseases (clinically called "metabolic" diseases), and mental ailments, as well as the contagious ones with which we are concerned here. The phenomenon of infectious disease is simply the result of parasitism, and indicates that some form of life is obtaining its nourishment from some other form at the expense of its host's well-being.

VII. HOW MICRO-ORGANISMS CAUSE DISEASE

Three factors make it possible for these pathogenic organisms, tiny as they are, to be effective in incapacitating and killing organisms as large as man, and larger. The first is their previously noted prodigious rate of multiplication, enabling them to increase their numbers to countless billions within a few hours, and to place a tremendous material burden on the tissues. The second is their ability actually to destroy tissues of the body, thus interfering with the source of important functions. But perhaps more deadly than either of these is their third method of attack—the production of poisonous substances, known as **toxins**. A toxin usually affects one particular organ or organ system—the central nervous system or the red blood cells, and so forth—rather than the body as a whole, thus producing a characteristic set of **symptoms** by means of which the physician can diagnose the disease and the organism responsible.

These chemical substances which bacteria* produce are of two types, called **exotoxins** and **endotoxins**. An exotoxin is an extremely potent poison secreted by the bacterial cell to the *outside* environment. A mere 0.002 cc. of diphtheria toxin is lethal for a guinea pig, as is 0.0005 cc. of tetanus (lockjaw) toxin, and 0.0001 cc. of botulinus (food poisoning)

* In regard to this third factor, we are speaking *primarily* of bacteria. Some viruses do give off toxins, but most of them, so far as is known, simply invade tissue. Rickettsias, too, act primarily by invading tissue, although some as yet unsubstantiated evidence indicates that some do give off toxins.

toxin. Why these proteins are so poisonous is unknown, for they do not seem to differ in any essential way from completely harmless ones, such as egg albumin. It may be that they block some fundamental chemical process of the cell, or they may function as enzymes to destroy some essential part of it. Whatever the explanation, they are easily destroyed by heat and enzymes (the botulinus poison is an exception to this, so that it alone of the exotoxins is effective when eaten, the others being destroyed by the digestive enzymes).

The other type of toxins, endotoxins—not all of which are proteins—are made and kept *within* the bacterial body, and released only after the bacterium dies and dissolves. These are not so powerful as exotoxins, but neither are they so easily destroyed by heat and enzymes.

Each kind of pathogenic bacterium both invades tissues and produces a toxin to some extent, and they can be arranged in a series, from the botulinus organism, which is very toxic, but least invasive,* through tetanus, diphtheria, streptococcus, and staphylococcus bacteria, to the tuberculosis bacillus, which is not very toxic, but invades and destroys tissues extensively.

Bacteria are not unique in producing toxins. Substances similar to exotoxins are found in the seeds of certain plants, such as the castor oil bean, and in the secretions of certain animals, such as the rattlesnake and cobra, the scorpion and black widow spider.

VIII. BODY DEFENSES AGAINST DISEASE

Against these weapons of pathogenic organisms the body is armed with a highly effective first line of defense, in the form of the skin, mucous membranes and digestive tract lining. Bacteria cannot ordinarily penetrate the skin, unless a break is provided by a wound. Sometimes they enter by way of the sweat gland ducts or hair follicles, but they are not often able to reach deeper tissues by these routes. Furthermore, the skin can actively destroy many kinds of bacteria, although its ability to do so is reduced by the presence of dirt, and ceases completely within fifteen minutes after death. The sticky mucus secretions of the digestive tract, nose and lungs are efficacious in preventing the spread of bacteria, by trapping them, while the mucous membranes themselves serve as mechanical barriers to their entrance. Still another barrier lies in the ciliated cells of the upper passages of the respiratory tract, whose constant beating moves the bacteria up towards the pharynx, where they are swallowed. In the stomach the majority of organisms are destroyed by the gastric juice, but a few, protected perhaps by a particle of food, survive and multiply in the intestine. These are constantly being eliminated with the feces. Both male and female urethras are normally quite free of bacteria, owing to the constant flushing by the slightly acid urine. The normally acid, vaginal secretions are lethal for most species of bacteria.

If disease organisms are successful in penetrating these first lines of

* Usually this anaerobic organism does not itself invade the body. Its toxin—the most deadly of all—is taken into the body via improperly canned food, and is lethal almost immediately. From this it is obvious that botulism is not a contagious disease, like all the others discussed in this chapter.

defense, other mechanisms come into play to control them. One of these is the process of **inflammation,** effective in localizing an infection. The presence of foreign bodies stimulates a dilatation of the capillaries (hence the reddening of the area), and the increased blood supply brings blood-clotting elements and white cells to combat the invaders. The formation of a clot traps them so that they cannot spread, while connective tissue fibers grows around the periphery of the clot and wall them off. The pus of an infection such as a pimple or boil consists simply of masses of bacteria in the process of being engulfed by white corpuscles. How the lymph nodes function in preventing the spread of infection has already been discussed (Chap. 9). When the body is in poor condition, owing to anemia, lack of vitamins, previous infectious diseases, or any other cause, it obviously cannot be so effective against invasion by disease organisms. This is why some people seem to get one thing after another, while others seem invulnerable to disease.

13. Acquired Immunity. In the eighteenth century many people, feeling sure that they would contract smallpox at some time in their lives, exposed themselves deliberately in order to have it at their convenience and get it over with. Even today some parents expose their children to childhood diseases from the same motive, because they know that certain diseases do not occur twice in a lifetime. This type of resistance —the body's last line of defense—is known as **acquired immunity.** But a person immune to smallpox, from having been a victim of it, is no more immune to measles or any other disease than someone who has never had smallpox, and for this reason we say that immunity is *specific.*

Actively acquired immunity depends upon the body's release of certain chemicals, called **antibodies,** into the blood and tissue fluids, after the invasion of some foreign protein, called an **antigen.** These two chemicals —antigen and antibody—react upon each other with the result that the body is protected from injury. For example, if some egg albumin (a protein) is injected into a rabbit, the animal's cells respond by producing antibodies specific for albumin, both then and forever after. Similarly, the body can produce a particular kind of antibody, known as an **antitoxin,** in response to the presence of a toxin (usually protein) released by a bacterium. When enough antitoxin has been produced, the body is no longer affected by that particular toxin. Some of the nonprotein endotoxins do not stimulate antibody production, and therefore are more dangerous to the body.

Antibodies react to the offending antigen in several different ways. They combine with some toxins, neutralizing their poisonous qualities; in other cases they dissolve the bacterial cells; or they may sensitize the bacteria, making them more vulnerable to the white corpuscles. Sometimes they agglutinize the organisms, thus preventing their spread, and making their entrapment by the lymph nodes more certain. Finally, they may precipitate the molecules of a toxin and render them inactive.

Another, more pleasant way in which immunity may be acquired is through **inoculation** with a **vaccine,** which we have mentioned already in connection with Pasteur. A vaccine is the commercially produced antigen of a particular disease, strong enough to stimulate the body to make antibodies, but not sufficiently strong to cause the disease's harm-

ful effects. Toxicity of the antigen is reduced in various ways. In some vaccines only a small amount of the toxin is present. In others both the toxin and the antitoxin are combined, so that while the antigen stimulates the body to produce more antibodies, the antibodies of the vaccine act as protection for the cells. Still other toxins are heated or treated chemically to destroy their deleterious properties, without destroying their ability to stimulate antibody production: such a vaccine is known as a **toxoid.** Another method is to attenuate the cultures of bacteria by growing them for long periods of time in test tubes, until they have lost some of their toxicity. Rabies vaccine is attenuated by drying, others by injection into a series of laboratory animals. Typhoid vaccine may be prepared with the use of dead typhoid bacteria.

The vaccination technique was discovered late in the eighteenth century by the English physician Edward Jenner, when he noticed that dairy workers handling cows with cowpox, never had smallpox. When he tried scratching some serum from the pustules on a cow's udder into a human being, a mild disease resulted, with a single localized pox at the point of injection. Men so vaccinated never acquired smallpox. It is now known that the same virus causes smallpox in human beings and cowpox in cows, but in the cow's body it becomes attenuated so that, when introduced into a human being, it produces a mild disease resembling cowpox, and confers immunity to the more serious disease. Theoretically, it should be possible to immunize against all diseases by inoculations, but the means for doing so have not been developed for many important diseases, among them tuberculosis, infantile paralysis, influenza and syphilis.

When a person has contracted a disease and needs antibodies immediately to combat its antigens, his body may not be able to manufacture them quickly enough. In such cases, antibodies produced by some other animal—usually a horse—are injected to tide him over until his own body can produce enough to protect him. The injection of prepared antibodies (called a **serum**) is the only method of *passively* acquiring immunity; although immediately effective, it disappears entirely after a few weeks.

To prepare a serum, bacteria are first cultured in test tubes until they have produced a large amount of toxin. This is then injected, in increasing doses, into a horse, which responds by gradually building up a tremendous amount of antitoxin in its blood. Finally, blood is withdrawn from the animal at intervals and processed to remove the blood cells and concentrate the antitoxin.

14. Natural Immunity. For all animals and plants, immunity to certain diseases is a part of their heritage and does not have to be acquired. For example, human beings cannot "catch" chicken cholera, because they have antibodies for its antigen. There is evidence that the various races of man differ hereditarily in their resistance to such diseases as tuberculosis, diphtheria and influenza. Hereditary invulnerability to disease is called **natural immunity,** and is passed on to each new generation.

One type of natural immunity is that built up in a population which has been exposed to a particular disease for many generations. Many

diseases, such as measles, which are relatively mild in civilized nations today, were extremely virulent among the American Indians and South Sea Islanders when they first came into contact with them. Syphilis, too, is a much milder disease now than at the time of its introduction into Europe, when it often was fatal in less than a month. And many tropical diseases, such as malaria and sleeping sickness, are severer for white men than they are for the natives. Other diseases, originally widespread, have become rare with the passage of time—leprosy, for example, was extremely frequent in biblical times.

This progressive change is usually interpreted as being the result of a gradual process of "natural selection." Thus people who survived in the early days of the disease passed on their "survival ability" to their offspring, and so on. It is possible, also, that in some diseases the micro-organism itself has undergone an adaptation, resulting in a decrease of virulence.

15. Allergy. Similar to the antigen-antibody reaction of immunity, is another, responsible for the type of hypersensitivity called **allergy,** which is expressed in such conditions as asthma, hay fever, skin rashes, and so on. This is due to the fact that any protein (antigen) which gets into the body not only stimulates the production of antibodies specific for it, but changes the reactivity of the cells. Then, if it enters the body again (at any time after about two weeks), its presence provokes any one or several of a multitude of symptoms: nausea, weakness, lowered temperature, convulsions and even death. Such symptoms are the outward signs of the body's fight against the antigen. An allergy, like immunity, is highly specific for a particular protein. Sometimes the unpleasant symptoms disappear after the reaction to the second invasion, but often they recur for years or even throughout life, whenever the antigen is present. Desensitization may be accomplished by successive injections of minute amounts of the antigen.

Perhaps the most common of all allergies is that involving the pollen of certain plants—roses, goldenrod, ragweed, and so on—known as hay-fever, rose fever, and the like. The protein antigen of the pollen enters the body through the mucous membranes of the nose or mouth and causes a sensitization. When, later, more pollen comes into contact with these membranes, they become swollen and irritated, and all the symptoms of a cold result.

Allergy to a particular kind of food is initiated when some undigested protein passes through the lining of the digestive tract (via a cut or lesion in the wall), and on into the blood stream. After sensitization to the protein has occurred, the next time the person eats the food he may become nauseated, or have hives, or some other reaction.

To test for an allergy, a small amount of sterile solution of a particular protein is injected into the patient's skin. If he is allergic to the protein, a large, localized, inflamed area appears, owing to the antigen-antibody reaction. The greatest care must be exercised that the test solution does not get under the skin, where it might come into contact with the blood stream and sensitize the person to the substance if he is not already sensitized.

It should hardly be necessary to say that, although allergies are a

form of disease (asthma is an example of how devastating they may be), they are not infectious,* since they are not caused by organisms. We include them in this chapter because the mechanism responsible for them is similar to that of immunity.

IX. THE SPREAD OF MICRO-ORGANISMS

Naturally, the number of deaths each year due to infectious diseases has decreased steadily and markedly since the discoveries of Pasteur and Koch. The explanation of this lies partly in the discovery of better methods of treatment—the use of antitoxins, sulfa drugs, penicillin, streptomycin, aureomycin and so on—but even more in our increasing efforts to prevent the *spread* of micro-organisms. To infect a new host there must be some way for organisms to get from one person to another, and since most of them can exist for only short periods of time outside the body, usually the best way to eliminate contagious diseases is to eliminate the means whereby the causative agents are transmitted. The Federal Government, the individual states, and many cities and counties have departments of Public Health, whose task is the prevention of infectious diseases by the enforcement of quarantines, inspection of food supplies, elimination of insect pests, testing of dairy herds, supervision of milk pasteurization, filtration and chemical treatment of water supplies, and sanitary disposal of sewage. These measures, which were possible only after scientists had learned enough about micro-organisms to determine how they could be attacked, now help protect us from the terrible epidemics or plagues of former ages.

Many microbes can pass from man to man only by the immediate contact of the two. In such cases isolation or quarantine of diseased persons is an effective way of preventing the spread of the disease. Quarantines were used long before the nature of disease was understood, for man early discovered that some illnesses were contagious. But even the strictest quarantine measures fail to prevent some spread of disease because many people are what is known as "immune carriers," infected persons who have antibodies protecting them from the harmful effects of the organisms, and thus the appearance of disease symptoms. In any disease epidemic several times as many people have a mild case, and perhaps never know that they have had it, as those who suffer the severe, recognizable form. Immune carriers can, of course, transmit the micro-organisms to others who are susceptible, and so unconsciously infect them. Typhoid, diphtheria, pneumonia and infantile paralysis are spread to a large extent by immune carriers.

Today, the number of people suffering from typhoid is less than a hundredth of what it was in 1890, owing chiefly to the use of chlorine and other disinfectants in drinking water. The drinking water of American cities is so pure that inoculation for typhoid is unnecessary except in emergencies, such as floods, when the water is likely to become contaminated.

Most of the milk sold in American cities has been pasteurized, or heated to a temperature of 145° F. for thirty minutes. This treatment

* Nor are they inherited, although a tendency to be easily sensitized (to make antibodies readily) may be inherited.

kills all the harmful bacteria known to be transmitted by milk: the germs of diphtheria die at 129°, those of typhoid at 136° and those of tuberculosis at 138° F. But some harmless bacteria survive the treatment, so that milk is not sterile and will turn sour if left in a warm place. And of course any harmful organisms which get into it after pasteurization multiply rapidly, for milk is an excellent culture medium for most bacteria.

Perhaps the greatest single reason for the decrease in contagious diseases is simply the increasing tendency toward general cleanliness—the increase in bathing, and the more careful handling of food, disposal of garbage and sewage, and the like, are all measures destructive of bacteria which otherwise might get into the body.

X. SOME COMMON INFECTIOUS DISEASES

16. Infantile Paralysis. The causative agent of infantile paralysis is a filterable virus, which enters the body either through the nasal membrane to the olfactory nerves, whence it passes to the brain and spinal cord, or by the digestive tract, whence it passes to the nervous system via the blood stream. Recent electron microscope studies at the Massachusetts Institute of Technology have shown that the virus passes along the nerves through ultramicroscopic nerve tubules, bundles of which constitute each single axon. It attacks and destroys these nerve cells, particularly those of the motor nerves, thus causing paralysis of certain parts of the body. Withering of the limbs, however, is caused only indirectly: because they are paralyzed and hence unusable, the muscles atrophy from lack of exercise. In common with most virus diseases, there is no satisfactory laboratory test for infantile paralysis, and diagnosis in the early stages is difficult because many of its symptoms resemble those of a bad cold. Nor is there any method for curing it; present treatment consists in keeping the patient in bed and well nourished so that a maximum of his energy can be used for combating the disease. Since it is spread by the coughing and sneezing of infected persons, prevention is aided by their segregation, which is the reason why all public assemblies are forbidden during severe epidemics.

17. Typhus. A rickettsia transmitted to man by rat fleas, or lice infecting either rats or humans, is the cause of one of the great plague diseases, typhus. Usually associated with filth and overcrowding, epidemics often follow the disruptions of war, and after World War I, 25,000,000 cases occurred in Russia alone. That such an epidemic did not accompany World War II was primarily due to the extermination of fleas and lice by liberal use of the insecticide DDT. The disease begins with a violent headache and fever, followed by prostration and the eruption of red spots. Frequently it is lethal, the fatality rate varying from 5 to 70 per cent during different epidemics. There is a diagnostic test for it (the Weil-Felix reaction) which depends on an antibody-antigen reaction, but there is no satisfactory treatment.

18. Syphilis. This disease was not recognized in Europe before 1493, and its origin has always been a matter of dispute: some have maintained that it was brought back to Europe from the New World by Columbus' crew; others, that it was already present in Europe. At any

rate, some of Columbus' crew accompanied King Charles VIII of France on his invasion of Italy in 1494, and the epidemic which started in Italy at that time spread over Europe as the troops scattered at the end of the war. The French called it the Italian disease, and, naturally, the Italians called it the French disease. It derives its present name from the principal character in a poem by Fracastorius, written in 1530, which described the then current methods of treatment with sulfur and mercury.

Its causative agent is a long, tightly coiled bacterium, called a spirochete (Fig. 195), which usually is brought into the body by the contact of the mucous membranes of the penis and vagina during sexual intercourse. It may possibly be contracted occasionally by indirect means, if a person puts to his mouth something which has just been in contact with the mouth of a syphilitic.* Or syphilis may be present

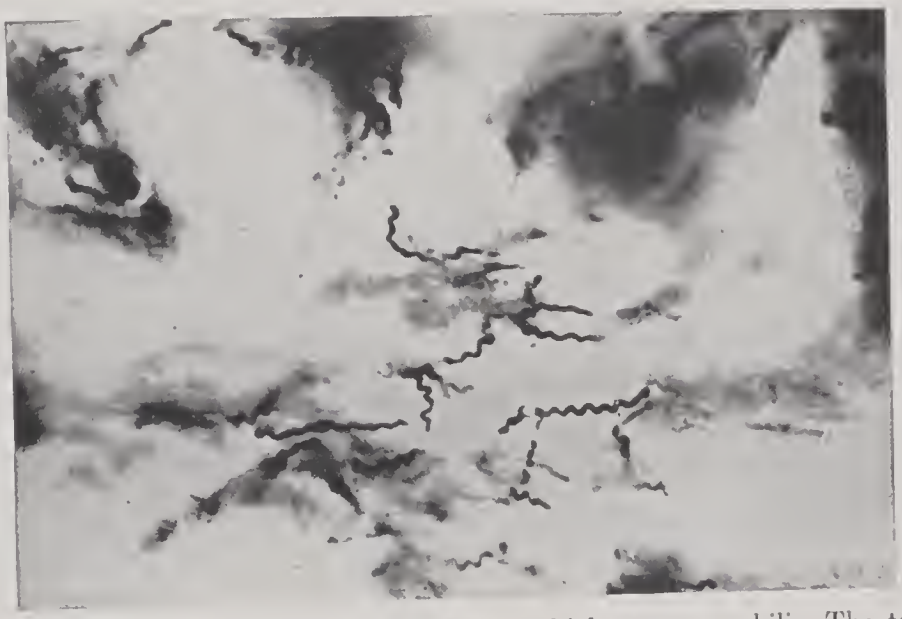


Fig. 195. The spirochete, *Treponema pallidum,* which causes syphilis. The typical corkscrew shape is evident. Magnified 2000 times. (Kral, in Burrows, W.: Jordan-Burrows Textbook of Bacteriology.)

from birth, transmitted by an infected mother to her child either before or at the time of birth.

The infection proceeds through three stages. In the *primary stage* a superficial lesion or sore appears on the external genitalia, or point of contact, ten to thirty days after infection. This is often small and painless and may be overlooked. The first stage lasts a few weeks only, and is followed by a long *secondary stage,* lasting months or years. During this period the spirochetes spread through the blood stream to other parts of the body, causing additional sores and lesions. But a long time may pass during which there is no external evidence of infection, so that a patient may think he is cured when he is not. If he is not cured, the *tertiary stage* occurs after several years and usually is fatal. All the organs of the body, and especially the central nervous system, may be attacked, resulting in paralysis and insanity due to the destruction of the nerve cells.

* Medical opinion is divided as to whether syphilis is *ever* contracted indirectly. Almost certainly ninety-nine cases out of a hundred are contracted directly, and probably the hundredth as well.

As you might expect, diagnosis varies according to the stage of the disease. In the first stage, demonstration with the aid of a darkfield microscope of the presence of spirochetes in the chancre or sore is a positive test. In the secondary and tertiary stages the famous Wassermann test, or one of its refinements, is used. The Wassermann test, which is based on an antigen-antibody reaction, cannot be used in the primary stage because the antibodies do not develop until two or three weeks after infection. For many years, treatment of syphilis depended upon repeated injections of the chemical salvarsan, or one of its derivatives, containing arsenic. The discovery of this chemical, which is poisonous enough to kill the spirochetes, but not sufficiently toxic to kill the patient, was the result of a long process of trial and error, carried on by the German physician Ehrlich. Treatment with salvarsan is still standard procedure, although it is supplemented now with the administration of penicillin, and the artificial induction of high fevers which kill the spirochetes.

The prevalence of syphilis in the United States varies widely in different parts of the country and among different groups of people. In one random series of autopsies, it was found in about 5.5 per cent of the total 150,000 cases. Of the first two million men drafted in World War II, 2.3 per cent of the whites, and 27.2 per cent of the Negroes, were infected. Since spirochetes cannot live outside the body, syphilis could be abolished by the discovery and treatment of every infected person—a program which has been remarkably successful in some of the European countries, notably Denmark and Sweden. The difficulty lies in getting everyone to take a Wassermann, and in persuading those infected to continue treatment until they can no longer infect others.

19. Athlete's Foot. This widespread, irritating, but usually harmless disease is transmitted from person to person in public showers, or similar damp places. Spores of the fungi from an infected person are deposited on the moist floor and picked up by the next one to step there. Diagnosis can be made by microscopic examination of scrapings from the infected parts, but ordinarily this is not necessary, for the symptoms are common and easily recognizable. The fungus usually grows between the toes, where the skin is soft and moist, but sometimes it appears on the soles of the feet, the hands, or even in the scalp or beard. The first signs of it are itching, and tiny blisters which break, exposing the raw, pink underskin. Spreading is usually slow and gradual. Athlete's foot can be cured by the application of weak acids, and can be prevented by the use of fungicidal baths in locker and shower rooms, and by thorough drying of all parts of the body after bathing.

20. Amebic Dysentery. Amebic dysentery is well known as a "traveler's disease," because it is often picked up by the unwary foreigner in countries where human feces are used for fertilizer. It is also common around army bivouacs and on board merchant marine vessels, and it even occurs from time to time in the United States. In short, people suffer from it whenever conditions of sanitation are poor.

The agent causing amebic dysentery is the ameba, *Endamoeba histolytica* (histo-tissue; lytic-dissolving), which gets into food in the form of cysts. In the stomach, the cysts dissolve, releasing the active amebas,

which attach themselves to the tissues of the large intestine, causing ulcers which interfere with the functioning of the colon, and consequently, diarrhea. Diagnosis of the disease is made certain when microscopic examination of the feces reveals the amebas and their cysts. It is treated by the administration of drugs to kill the ameba. Sanitation, including thorough sewage disposal and cleanliness in the preparation of food, is its only preventative.

21. Tapeworm Infections. The tapeworm, which has become a kind of joke, but is not at all amusing to those who have one, owes its name to its shape, which resembles a measuring tape, and may be from 6 to

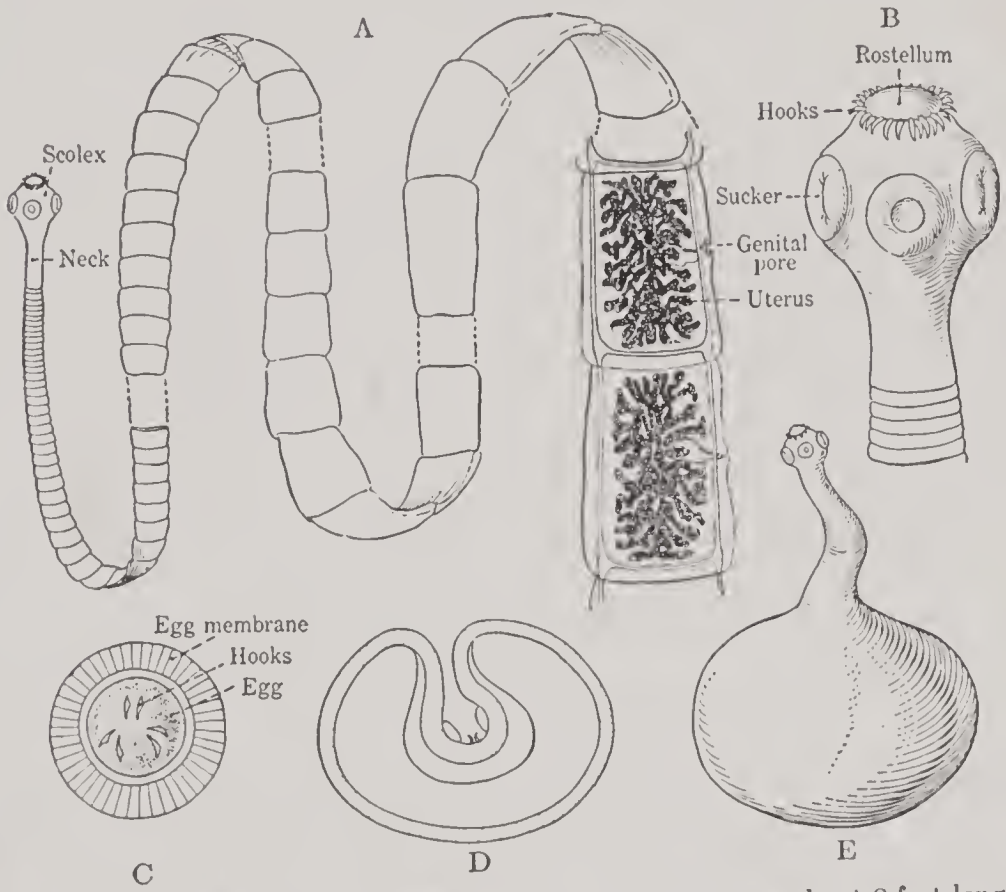


Fig. 196. The pork tapeworm, *Taenia solium*. The specimen was about 8 feet long. *A*, The anterior and posterior parts of the worm. *B*, An enlarged view of the head. *C*, An egg. *D* and *E*, The bladderworm stage. (Woodruff: Foundations of Biology, 6 ed., published by The Macmillan Co.)

30 feet long. The adult worm lives only in the digestive tract of man,* where it lays eggs, which it fertilizes itself (the worm is hermaphroditic) and which pass out of the body with the feces. The eggs are then eaten by an intermediate host—a hog or cow—in whose digestive tract the eggs grow into larvae. These bore through the wall of the intestine, enter the blood stream and are carried to the muscles, where they develop into small, cystlike "bladderworms" (Fig. 196). When the hog or cow is killed, and the meat is eaten without being cooked sufficiently to kill the bladderworms, the person becomes infected. The bladderworm passes into the intestine, rapidly matures into an adult, and fastens onto the wall of the intestine by hooks in its head. Here it remains, "soaking

* But there are many other species of tapeworms which infect probably every type of vertebrate.

up" digested food from its host (for it has no mouth and no digestive tract of its own) and consequently causing cramps, indigestion and malnutrition. Diagnosis of the disease depends upon the demonstration, by a trained laboratory technician, of tapeworm eggs in the feces. Treatment consists in administering drugs to kill or anesthetize the worms, followed by purges to flush them out. Prevention is effected by thorough cooking of all flesh eaten (other tapeworms are acquired from raw fish), by the disposal of sewage to prevent the infection of intermediate hosts, and by inspection of all carcasses destined for the market.

22. Trichinosis. The worm causing this disease differs from the tapeworm (they belong to different phyla) in being small and round. The larvae, which are minute, coiled worms, 1 mm. long, lie within the muscles of a hog, enclosed by lemon-shaped cysts (Fig. 197). When the

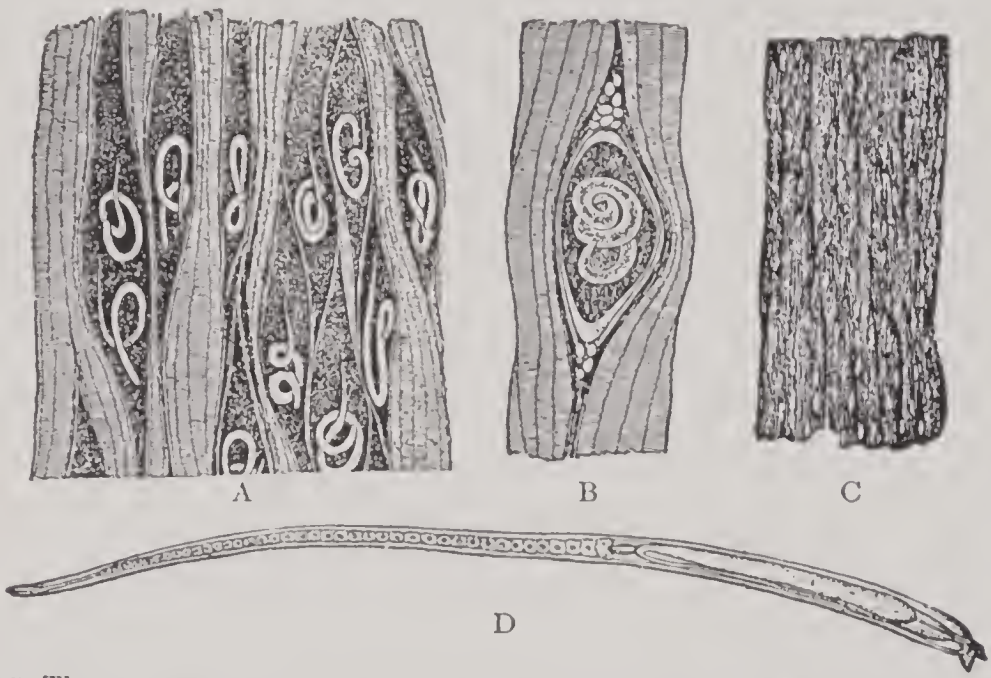


Fig. 197. The roundworm, *Trichinella spiralis*. *A*, Larvas burrowing among the muscle fibers. *B*, Single, encysted larva. *C*, Piece of pork containing many encysted worms, natural size. *D*, An adult worm, enlarged. (Woodruff: Foundations of Biology, published by The Macmillan Co.)

animal's flesh is eaten by a human being, if it is not thoroughly cooked, the cysts are digested away in the stomach and the worms enter the small intestine and mature in about two days. After a week or so, when the females' eggs have been fertilized by the males' sperm, the females deposit tiny larvae in the intestinal lining. From here, the larvae pass, via the blood stream, to the muscles, where they form cysts. There are, then, two distinct phases of the disease: the first, when the intestine is infected with the adult worms, which involves severe gastrointestinal disturbances and is sometimes fatal, and the second, which follows invasion of the muscles by the larvae and is characterized by muscular soreness.

Trichinosis is not directly transmissible from person to person (or could be so only through cannibalism), and the hogs themselves become infected by eating pork scraps, or rats which have eaten pork scraps. The disease can be diagnosed by an antigen-antibody skin test, but unfortunately there is no known cure. Government inspection of pork

does not include inspection for the trichinosis roundworm, which would be impractical, but the disease can be prevented by the thorough cooking of all pork products. Further preventive measures include outlawing the feeding of raw garbage to pigs and the elimination of rats from pig farms.

QUESTIONS

1. What role do bacteria play in returning the essential elements to general circulation?
2. What, in particular, do the "nitrate" bacteria do?
3. What are aerobic bacteria?
4. What is fermentation? How does it differ from putrefaction?
5. Differentiate between rickettsias and viruses. What are bacteriophages?
6. In what ways are fungi and bacteria alike? How do they differ?
7. What are antibodies? How do they combat disease?
8. What are the three types of disease? What is the cause of each?
9. What are the three factors which enable micro-organisms to operate well as parasites?
10. Differentiate between exotoxins and endotoxins; antigens and antibodies; vaccines and serums.
11. How does the body defend itself against the invasion of disease organisms?
12. Explain how serums are prepared.
13. What is the physiological explanation of allergies?

SUPPLEMENTARY READINGS

Frobisher, M.: *Fundamentals of Bacteriology*. 4th ed. Philadelphia, W. B. Saunders Company, 1949.
A clear, readable discussion of micro-organisms, their structure and physiology. The chemical aspects of bacteriology are stressed.

Henrici, A. T., and Ordal, E. J.: *The Biology of the Bacteria*. Boston, D. C. Heath & Co., 1948.
An up-to-date account of the biology and chemistry of bacteria.

Rahn, O.: *Microbes of Merit*. Lancaster, Pa., Jacques Cattell Press, 1945.
A popular book on bacteria.

Simmons, J. S.: *Global Epidemiology*. Philadelphia, J. B. Lippincott Company, 1944.
An interesting account of the relation of geography to disease.

Zinsser, H.: *Rats, Lice, and History*. Boston, Little, Brown & Company, 1935
A fascinating account of plagues and their influence on historical events.

PART VI

THE MECHANISM OF HEREDITY

CHAPTER 23

THE PHYSICAL BASIS OF HEREDITY

IN A SENSE, the study of heredity is one of the oldest divisions of biology, since it was recognized at an early time that "like begets like" and that new types of animals and plants may result when unlike forms are crossed. From prehistoric times, men have tried to breed better horses, dogs, cattle, vegetables and fruits. In another sense, the study of heredity is the newest biological science, for as late as 1900 the scientific basis of inheritance was largely unknown.

New organisms closely resemble their parents: the offspring of a bean plant are always beans and nothing else; the mating of two cats always produces cats and no other animal. Furthermore, the mating of two Siamese cats always produces Siamese cats and not a different variety. Particular characters are frequently passed through a long series of generations in man as well as in other animals. This resemblance of individuals to their progenitors is called **heredity.**

The fact of heredity is so familiar that its significance is frequently overlooked. The sperm cells and the parts of eggs effective in inheritance, the nuclei, are both exceedingly small. All the sperm which gave rise to the present human population of the world could be contained in a single drop of water, and another drop could hold all the egg nuclei necessary. The living substance of the sperm and egg nuclei transmit all the characters which the new individual inherits from his parents. The qualities themselves—color, size, shape, and so forth—are not present in the germ cells, but something representing them and capable of producing them in the new individual is present. In man, the color of hair, eyes and skin, the size and shape of the body and its parts, certain structural defects, resistance to various diseases, certain mental traits, capacities and defects are all inherited and therefore must be represented in the gametes. The latter, then, contain factors which interact with each other and with the environment to produce the adult characteristics. These hereditary factors are among the most remarkable things in existence.

Although resemblances between parents and offspring are close, they are usually not exact. The offspring of a particular set of parents differ from each other and from their parents in many respects and to different degrees. This is clearly evident among human beings; in other animals and among plants it is not always immediately obvious, but detailed studies usually bring the dissimilarities to light. These differences, termed **variations,** are characteristic of living things. It is often said that variation is the most invariable thing in nature. Some variations are inherited, that is, caused by the segregation of hereditary factors among the offspring; others are not inherited, but are due to the effects of temperature, moisture, food, light and other factors in the environ-

ment on the development of the organism. Most characteristics are strongly influenced by the environment in which the individual develops.

The branch of biology concerned with the phenomena of heredity and variation and the study of the laws governing similarities and differences between individuals related by descent, is called **genetics.** Since its inception at the beginning of this century, the science has advanced rapidly and is still developing.

Although rather hit-or-miss efforts at breeding domesticated animals and plants had been carried on for centuries, and breeding procedures, such as the artificial pollination of the date palm, were performed in Egypt and Mesopotamia centuries before the Christian era, scientific understanding of the processes of heredity and variation had to wait until knowledge of the details of sexual reproduction existed. Only after the invention of the microscope and the recognition of spermatozoa by early microscopists, the demonstration early in the eighteenth century that spermatozoa initiate development, and the demonstration in the latter half of the nineteenth century that eggs and sperm are single cells whose nuclei fuse in fertilization, could the science of genetics arise.

Throughout the eighteenth and nineteenth centuries many investigators tried to discover how characters are transmitted from generation to generation. From about 1760 to 1770, the German botanist Kölreuter experimented with crossing two species of tobacco by placing pollen from one species on the stigmas of the other. The resulting hybrids had characters intermediate between those of the two parents. This indicated that parental characters are transmitted through both pollen and ovule. Kölreuter and the plant hybridizers who followed him failed to discover the nature of the hereditary mechanism partly because the cytological basis of heredity was unknown and partly because they tried to study the inheritance of all the characters of the plants involved, at once.

Gregor Mendel, an Austrian abbot who performed experiments in the garden of his monastery at Brunn, Austria, succeeded where previous hybridizers failed because he studied the inheritance of single contrasting characters (such as green versus yellow seed color, wrinkled versus smooth seed coat in peas), counted the number of each type, and kept accurate records of his crosses and counts. His experiments showed that inheritance is subject to certain laws, and that if the pedigrees of two individuals are known, the types of offspring produced by mating them can be predicted with a high degree of accuracy. His results, published in an obscure Austrian journal in 1868, aroused little interest in the scientific world, and were neglected for more than thirty years.

In 1900, after the details of fertilization had been discovered, three investigators, de Vries in Holland, Correns in Germany, and von Tschermak in Austria, independently rediscovered the laws of inheritance described by Mendel. In searching through the literature, they found his paper, and so, sixteen years after Mendel's death, the two fundamental laws of inheritance were named after him. To understand these laws and their application to heredity, we must first consider the mechanism inside the cell which is responsible for inheritance.

From the chapter on development, you will remember that the growth of an individual plant or animal is due to cell division plus the growth

of each cell comprising the organism. This division of cells is a regular process, exactly following a certain plan; it is known as **mitosis.** Under rare, usually pathological, conditions, a cell may split irregularly, without following the exact plan; this is called **amitosis.**

1. Chromosome Structure. When a cell undergoing mitosis has been stained for inspection under the microscope, its **chromosomes** are visible as dark bodies. These contain the factors controlling inheritance. All chromosomes have a definite size and shape, and particular ones can be recognized by the trained investigator. Each one consists of a central thread called a **chromonema,** along which lies a series of beadlike structures, the **chromomeres.**

The chromosomes are distinctly visible as just described, only during cell division; at other times they appear as fine strands called **chromatin,** which are also dark-staining. Research has shown that the chromosomes are present as distinct physiological and structural entities between successive cell divisions even though in most forms they are not visible.

When the chromomeres were first seen, many biologists believed them to be the **genes,** the hereditary factors which previous breeding experiments had shown to lie within the chromosome in a linear order. More recent research has shown, however, that there is no one-to-one correspondence between chromomeres and genes; that is, there is not a single gene for each chromomere. Instead, some chromomeres contain several genes, and some genes have been located between chromomeres. The exact significance of these swellings along the chromonema is not clear.

2. Chromosome Number. Each cell of every organism of a given species contains a definite number of chromosomes. The number for man is forty-eight—thus, every cell in the body of every human being has exactly forty-eight chromosomes (Fig. 198). Many other species of animals and plants also have forty-eight; so it is not the *number* of chromosomes alone that differentiates the various species of animals but chiefly the nature of the hereditary factors in the chromosomes. A certain species of roundworm has only two chromosomes in each cell, and some crabs have as many as 200 in each cell. The highest chromosome number reported so far is about 1600, found in a radiolarian, a microscopic, single-celled marine animal. Most species have a chromosome number between ten and fifty; numbers above and below this are comparatively rare. *Chromosomes always exist in pairs;* there are invariably two of each kind. Thus, the forty-eight chromosomes of man consist of two of each of twenty-four different kinds. They differ in length, shape and the presence of knobs or constrictions along their length. In most species the chromosomes vary enough in these morphological features that the cytologist can pick out the pairs quite easily.

3. Mitosis. These facts explain why cell division must be a regular phenomenon. It is necessary for each of the daughter cells formed by a cell division to receive exactly the right kind and number of chromosomes. If we tamper with the mechanism of cell division in an experimental animal or plant so that cells receive more or less than the proper number of chromosomes, great abnormalities and even death may result. *Mitosis, therefore, is the regular division of a cell, in which each*

of the two daughter cells receives exactly the same number and the same kind of chromosomes that the parent had. This involves what appears and was long believed to be a longitudinal splitting of each chromosome into two halves. It is now believed that new ones are formed, not by the

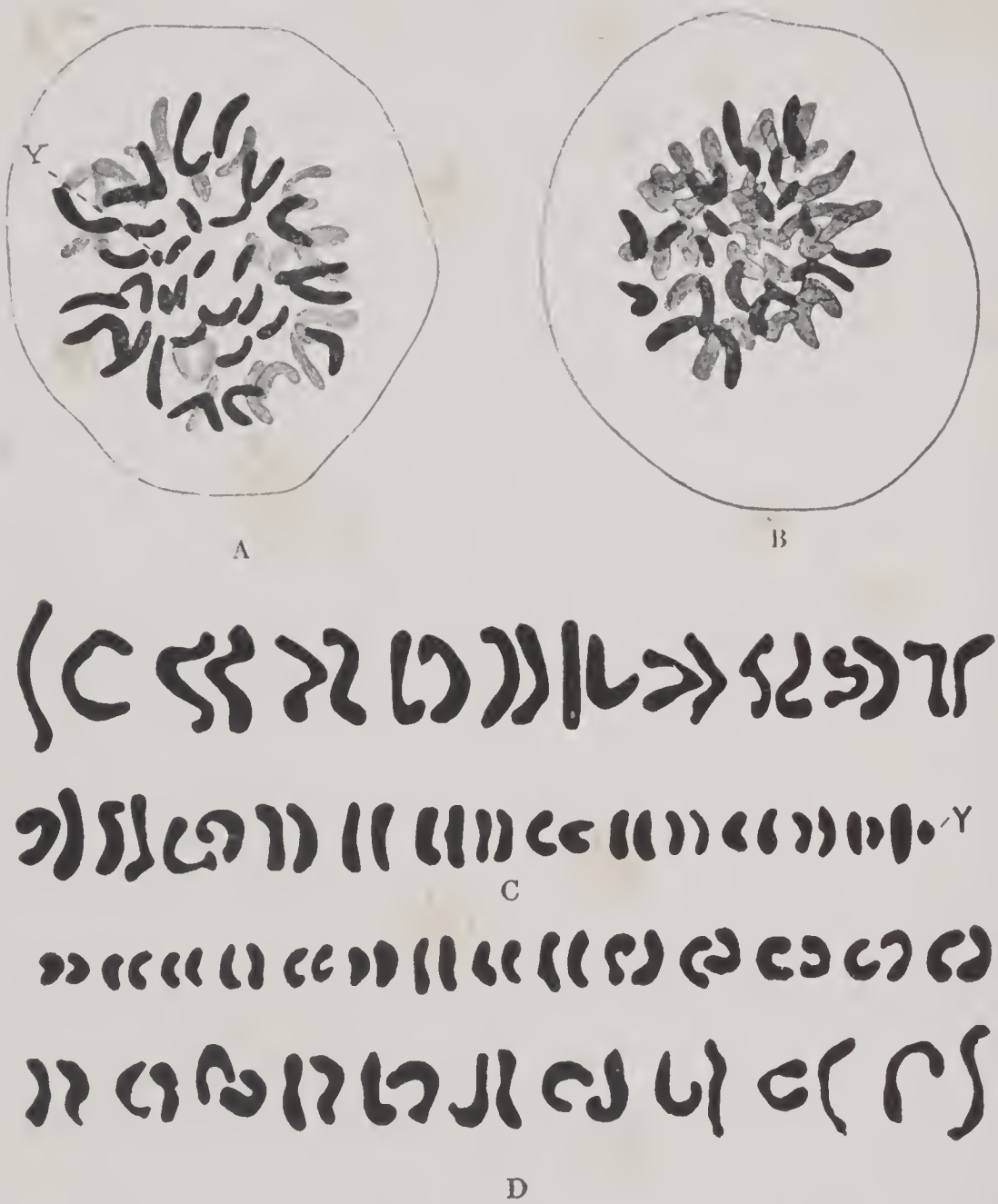


Fig. 198. Human chromosomes. *A*, Equatorial plate from a mesenchyme cell (male), showing the forty-eight chromosomes. The Y chromosome is indicated, *B*, Equatorial plate from a mesenchyme cell (female), showing the forty-eight chromosomes. *C*, The chromosomes from the prophase nucleus of a male, lined up to show the homologous pairs. *D*, The chromosomes from the prophase nucleus (female), lined up to show the homologous pairs. (Evans and Swezy: The Chromosomes in Man, Memoirs of the Univ. of California.)

splitting of the original chromosome, but by the building up by the chromosome of an exact replica of itself immediately beside it (a process known as **autocatalysis**). The new chromosome is manufactured from raw materials present in the cell nucleoplasm, but just when it is made is unknown; it may be before mitosis begins. The old and new chromosomes are identical in structure and function and at first lie so close to each other that they appear to be one. As cell division occurs, and the

chromosomes contract, the line of cleavage between them becomes visible and the chromosomes appear to split. In man, then, each of the forty-eight chromosomes synthesizes an exact replica of itself, so that for a time there are ninety-six chromosomes in the cell. Then cell division is completed, and forty-eight go to one, and forty-eight to the other daughter cell. A complicated mechanism is necessary to insure the equal division of the chromosomes.

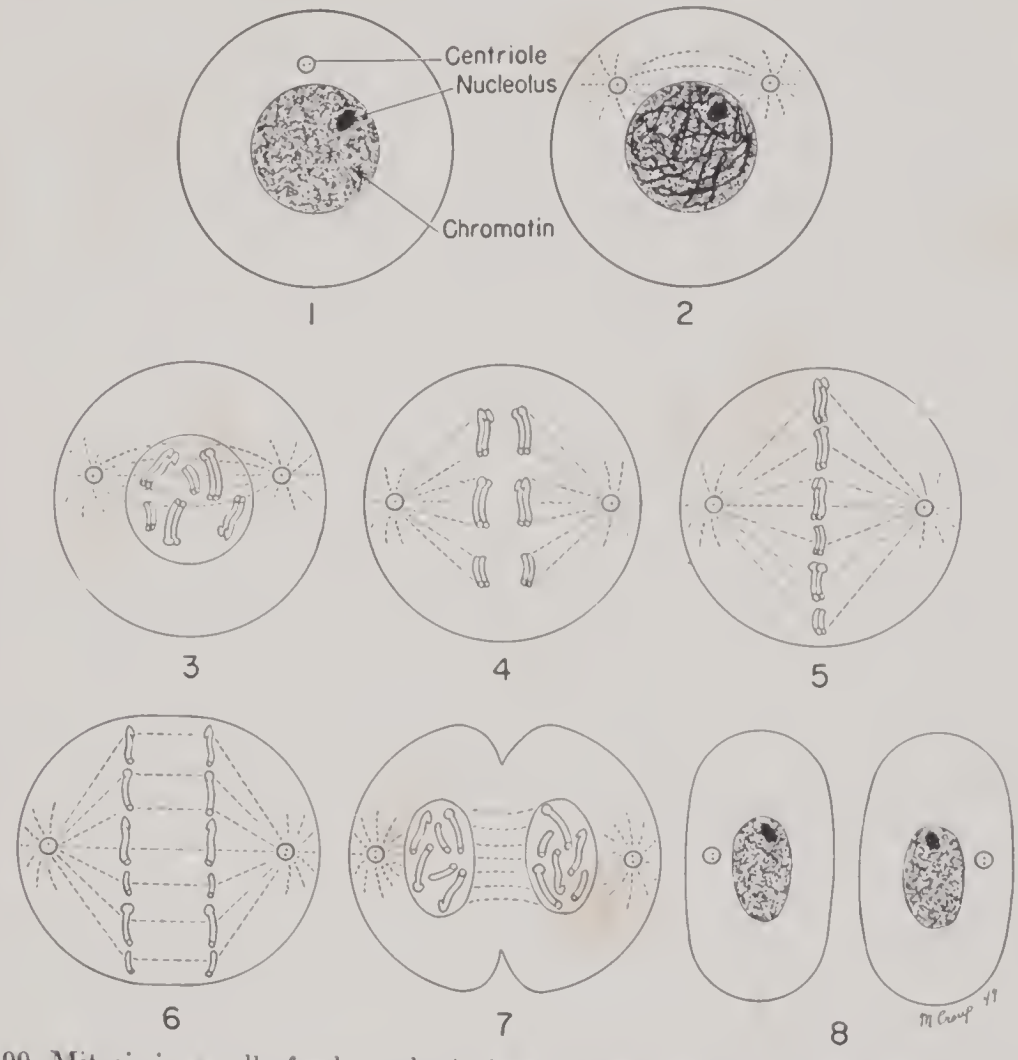


Fig. 199. Mitosis in a cell of a hypothetical animal with a diploid number of six (haploid number = 3); one pair of chromosomes short, one pair long and hooked, and one pair long and knobbed. *1*, Resting stage. *2*, Early prophase: centriole divided and chromosomes appearing. *3*, Later prophase: centrioles at poles, chromosomes shortened and visibly doubled. *4*, Late prophase: nuclear membrane dissolved, spindle present. *5*, Metaphase: chromosomes arranged on equator of spindle. *6*, Anaphase: chromosomes migrating toward poles. *7*, Telophase: nuclear membranes formed; chromosomes elongating; cytoplasmic divisions beginning. *8*, Daughter cells: resting phase.

Each mitosis is a continuous process, one stage merging imperceptibly into the next. However, for descriptive purposes, biologists have arbitrarily divided it into four stages: **prophase, metaphase, anaphase** and **telophase.** Between mitoses, a cell is said to be in the **resting stage** (Fig. 199).

Mitosis is an extremely active process. It is difficult to realize from a description, diagram or even from a prepared slide of cells undergoing mitosis just how active it is.

Prophase. In the prophase the chromatin threads begin to conde-

and form chromosomes, appearing as a tangled mass of threads within the nucleus. At first the chromosomes are stretched maximally and the individual chromomeres are clearly visible. In favorable conditions the chromomeres can be seen to differ one from another in size and shape, so that individual ones are recognizable. Later, the chromosomes contract and the chromomeres lie so close together that individual ones cannot be distinguished. Even at this early stage, each chromosome has undergone autocatalysis and in certain species its double nature is apparent.

The cell cytoplasm contains a small, granular structure called a **centriole.** At the beginning of prophase the centriole divides, and the daughter centrioles migrate to opposite sides of the cell. Between the separating centrioles a spindle forms, composed of a number of protoplasmic threads called **spindle fibers.** These are arranged like two cones put together base to base, so that the spindle is narrow at the ends or poles near the centrioles, and broad at the center or equator. The spindle fibers stretch from equator to pole and are composed of a denser protoplasm than the surrounding nucleoplasm. The spindle is a definite structure; by using a micromanipulator it is possible to introduce a fine needle into a cell and push the spindle around. While the centrioles have been separating and the spindle forming, the chromosomes in the nucleus have been contracting, getting shorter and thicker. Their double nature which may not have been visible before, can now be clearly seen.

Metaphase. When the chromosomes have contracted to their fullest extent, forming tiny, dark-staining, rodlike bodies, the nuclear membrane disappears (dissolves) and the chromosomes line up across the equatorial plane of the spindle, which has been forming around them (Fig. 199). At this point the prophase is complete, and the short period during which the chromosomes are in the equatorial plane constitutes the metaphase. When the division of living human cells is observed under the microscope, the prophase lasts from thirty to sixty minutes and the metaphase from two to six minutes. The times vary for different tissues and different species.

Anaphase. Now the chromosomes immediately begin to separate, one of the separating members (daughter chromosomes) going to each pole. The events from the time when the chromosomes first begin to move apart until they reach the poles constitute the anaphase, a period of three to fifteen minutes. The exact mechanism causing the chromosomes to move poleward is unknown. The earliest suggestion was of a pull exerted by the spindle fibers. According to another theory, the spindle fibers merely act as tracks or guiderails along which the chromosomes glide in going to the poles. The motive power is supplied by protoplasm which gets between the daughter chromosomes, absorbs water, and swells, thereby pushing the chromosomes apart. If it were not for the spindle fibers, the chromosomes would be pushed at random in all directions. But with them, all of one set of daughter chromosomes are gathered at one pole, and all of the other set at the other pole. Another theory attributes the migration of the chromosomes to electrostatic repulsion.

Telophase. When the chromosomes reach the poles, the telophase

begins. This is a period roughly equal to the prophase, lasting thirty to sixty minutes. The chromosomes elongate, lose their dark-staining capacity, and return to the resting condition in which only chromatin threads or granules are visible. While this is happening, a nuclear membrane forms around each daughter nucleus, and, simultaneously, the cytoplasm begins to divide. In animal cells the division is accomplished by a furrow encircling the surface of the cell in the plane of the equator. The furrow gradually deepens and separates the cytoplasm into two halves, the daughter cells, each of which has a nucleus. In most kinds of cells the entire process of mitosis consumes from one to two hours. In plants, division occurs by the formation of a **cell plate**, a partition of cytoplasm which forms first in the equatorial region of the spindle and then grows laterally to the cell wall. The net result, in any case, is the creation of two cells from a previous one. Each daughter cell has exactly the same number and kind of chromosomes that the parent cell had: hence, through mitosis, each cell in the body comes to have the hereditary material necessary for every characteristic of the organism. Mitosis occurs with widely different frequencies in various tissues, and in different species. In the red bone marrow, for example, where 10,000,000 red blood cells are produced per second, 10,000,000 mitoses must occur per second. In other tissues, such as those of the nervous system, mitoses occur very rarely. During the early development of an organism, cell divisions take place extremely rapidly and may occur every thirty minutes.

4. Control of Mitosis. The factor which initiates mitosis is not known exactly, but the ratio between the volume of nucleus and cytoplasm (the nucleoplasmic ratio) is believed to be involved. The increase in the size of the cell is effected by the older protoplasm manufacturing new protoplasm from simpler raw materials. This involves the diffusion of substances back and forth through both nuclear and cell membranes. Although the volume of a sphere increases as the cube of its radius, the surface increases only as the square of the radius, so that, as the cell grows, the volume increases more rapidly than the surface of the nuclear membrane. Beyond a certain point, then, the surface of the nucleus is insufficient to allow the necessary exchange of materials between nucleus and cytoplasm to provide for future growth. A division of the nucleus greatly increases the surface without increasing the volume, and it is believed that this limiting factor in the nucleoplasmic ratio somehow initiates mitosis.

Some biologists have suggested that a hormone is involved in starting mitosis. Indeed, the mitoses of various cells in a cleaving egg occur simultaneously for a long time; perhaps a hormone is released periodically to control them. Even in adult organisms, mitosis in tissue cells may occur in waves, suggesting that some inductive substance, or hormone, is present. Haberlandt found evidence that dying cells may produce a substance to stimulate cell division. In his experiments he cut a potato in half and examined the cut edges for mitosis. He found that if he cleaned off the cut edge, few mitoses took place; if he did not clean off the cut edge, cell divisions were more frequent; and if he put a mash of cut-up potato cells on the cut edge, many more occurred. He therefore concluded that the cut-up and dying potato cells produced a "wound

hormone" which stimulated cell division and the formation of scar tissue. Some similar process may be present in animals.

Another suggestion as to the cause of mitosis has been given by Gurwitsch, who believes that growing tissues give off "mitogenetic rays" which stimulate cell division in adjacent tissues. These are supposed to be weak ultraviolet radiations. It is difficult to prove the reality of these rays, and many biologists doubt their existence.

5. Meiosis. Constancy of the chromosome number in successive generations is brought about by the process of **meiosis,** which occurs during the formation of gametes, either eggs or sperm. Meiosis is essentially a pair of cell divisions during which the chromosome number is reduced to half, in order that the gametes receive only half as many chromosomes as other cells in the body; thus, when two gametes unite in fertilization, the normal chromosome number is reconstituted. The reduction of the chromosome number in meiosis does not occur at random, but in a regular way; in man, twenty-four particular chromosomes go to each pole and become incorporated in each gamete. Chromosomes, you will remember, occur in pairs, and in man there are twenty-four pairs in the body cells. *As a result of meiosis, each gamete contains one and only one of each kind of chromosome—one complete set of twenty-four chromosomes.* This is accomplished by the pairing or **synapsis** of the like chromosomes, and a separation of the members of the pair, one going to each pole. The like chromosomes which synapse during meiosis are called **homologous chromosomes.** They are identical in size and shape, have identical chromomeres along their lengths, and contain similar hereditary factors or genes. A set of one of each kind of chromosome is called the **haploid** number; a set of two of each kind is called the **diploid** number. For man, then, the haploid number is twenty-four, the diploid, forty-eight. Gametes have the haploid number; fertilized eggs and all the cells of the body developing from the zygote have the diploid number. A fertilized egg gets exactly half its chromosomes (and half its genes) from its mother, and half from its father. Only the last two cell divisions which result in mature, functional eggs or sperm are meiotic; all other cell divisions are mitotic.

The process of meiosis consists of two cell divisions which occur in quick succession, called, respectively, the first and second meiotic divisions (Fig. 200). Each of these has the same four stages, prophase, metaphase, anaphase and telophase, found in mitosis. There are, however, important differences between mitosis and meiosis within these stages, particularly in the prophase of the first meiotic division. In this, the chromosomes appear as long thin threads condensing from chromatin, as in mitosis. They begin to contract, getting shorter and thicker. Early in this prophase, while the chromosomes are still elongated and thin, the homologous chromosomes undergo synapsis; that is, they pair longitudinally, coming to lie close together, side by side along their entire length and twisted around each other. After synapsis, the chromosomes continue to shorten and thicken. Each one then becomes visible as being double, consisting of two threads, as in mitosis. Again, the time of this doubling is unknown. It occurs by autocatalysis, the synthesizing of a new chromosome from simpler nuclear materials under the direc-

tion of the original chromosome. At the end of the prophase, then, the chromosomes have synapsed and doubled, yielding a bundle of four homologous chromosomes called a **tetrad.** Since each pair of chromo-

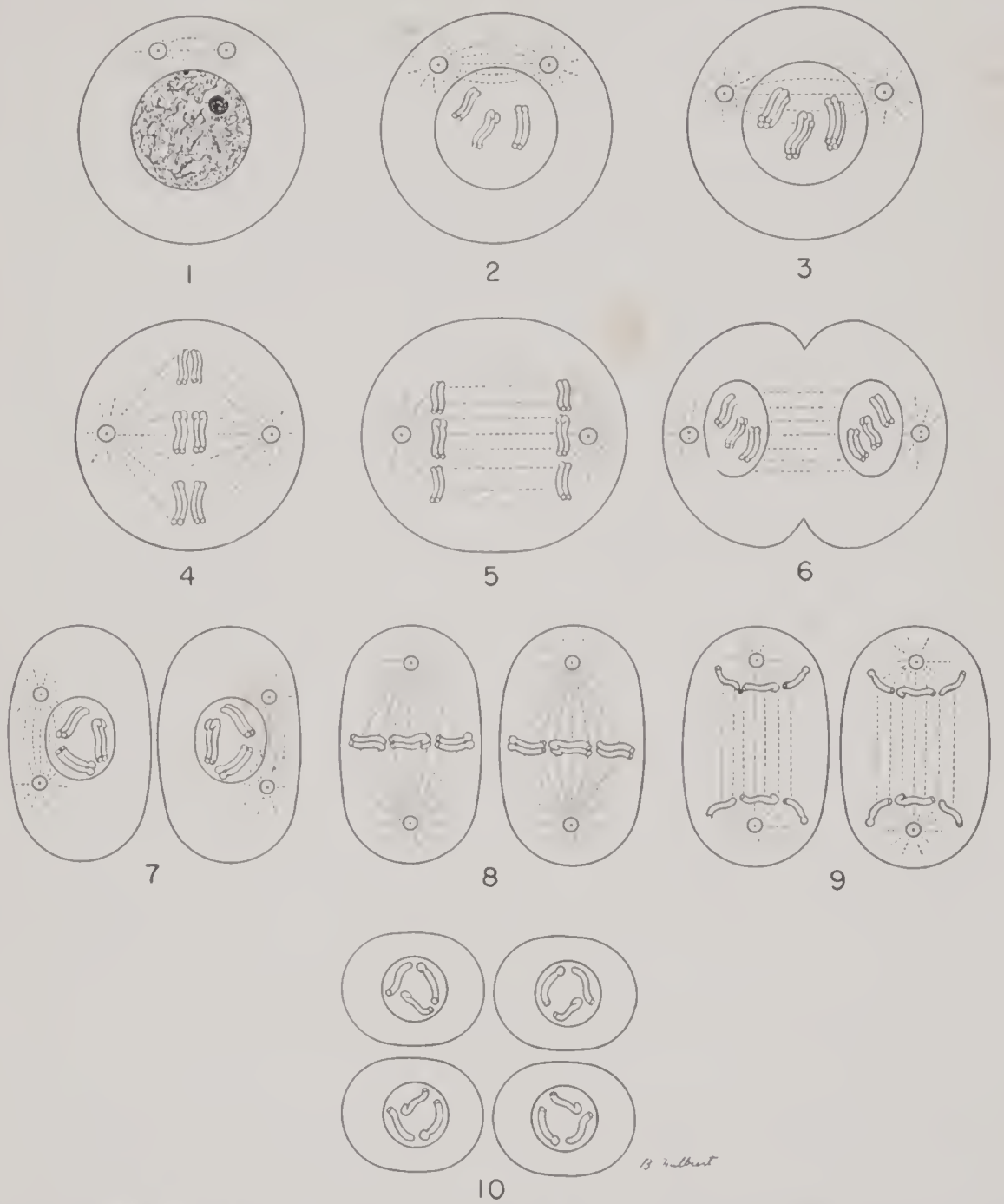


Fig. 200. Meiosis in a hypothetical animal with a diploid chromosome number of six. It has three pairs of chromosomes, of which one is short, one is long with a hook at the end, and one is long and knobbed. *1,* Early prophase of the first meiotic division: chromosomes begin to appear. *2,* Synapsis: the pairing of the homologous chromosomes. *3,* Doubling of the synapsed chromosomes to form groups of four identical chromosomes, tetrads. *4,* Metaphase of the first meiotic division, with the tetrads lined up at the equator of the spindle. *5,* Anaphase of the first meiotic division: the chromosomes migrating toward the poles. *6,* Telophase of the first meiotic division. *7,* Prophase of the second meiotic division. *8,* Metaphase of the second meiotic division. *9,* Anaphase of the second meiotic division. *10,* Mature gametes, each of which contains only one of each kind of chromosome.

somes gives rise to a bundle of four, there are as many tetrads as the haploid number of chromosomes. In human cells there are twenty-four tetrads and a total of ninety-six chromosomes at this stage.

While these events are taking place, others progress as in the mitotic

prophase: the centriole divides and the two centrioles go to opposite poles, the spindle forms between the centrioles, and finally the nuclear membrane dissolves. The tetrads then line up around the equator of the spindle, as the individual chromosomes do in mitosis, and the cell is said to be in metaphase. The homologous chromosomes now separate from each other and move to the poles. The doubled chromosomes do not separate; only the homologous ones which underwent synapsis do. Thus the chromosomes moving to the poles in the anaphase of the first meiotic division are double, and in the telophase of the first meiotic division in man there are twenty-four double chromosomes at each pole. The division of the cytoplasm follows, but in most animals and plants there is no resting stage between the two meiotic divisions. The chromosomes do not dissolve and form chromatin threads; instead, a new spindle forms in each cell (at right angles to the spindle of the first division), and the haploid number of double chromosomes line up on the equator of this spindle. Because of this, the telophase of the first meiotic division and the prophase of the second meiotic division are rather short. Of course, the lining up of the double chromosomes on the equator of the spindles constitutes the metaphase of the second meiotic division. It is possible to differentiate the metaphases of the first and second meiotic divisions when seen under the microscope, because in the first meiotic division the chromosomes are arranged on the equator in bundles of four (the tetrads), and in the second meiotic division in bundles of two. The two chromosomes now simply separate, moving to opposite poles without the occurrence of splitting or autocatalytic doubling, so that in the anaphase of the second meiotic division twenty-four single chromosomes (one of each kind) arrive at each pole. In the telophase that follows, the cytoplasm divides, the chromosomes gradually change back into chromatin, and a nuclear membrane forms. From these two successive divisions, four cells emerge, each with the haploid number of chromosomes, each with one and only one of each kind of chromosome. These are now mature gametes, and do not undergo any further mitotic or meiotic divisions.

Fundamentally, the same process occurs in the meiotic divisions in the testis resulting in sperm, as in the meiotic divisions in the ovary resulting in eggs, but there are some differences in detail which we shall discuss separately.

Spermatogenesis. The testis is made up of thousands of cylindrical sperm tubules, in each of which millions of sperm develop. The walls of these tubules are lined with primitive, unspecialized germ cells called **spermatogonia**. Throughout embryonic development and during childhood, the spermatogonia divide mitotically, giving rise to additional spermatogonia to provide for the growth of the testis. After sexual maturity, some of the spermatogonia begin to undergo **spermatogenesis**, the series of changes which results in mature sperm. Other spermatogonia continue to divide mitotically and produce more spermatogonia for later spermatogenesis. In most wild animals there is a definite breeding season, either in spring or fall, during which the testis increases in size and spermatogenesis occurs. Between breeding seasons the testis is small and contains only spermatogonia. In man and most domestic

animals, spermatogenesis occurs throughout the year once sexual maturity is reached.

Spermatogenesis begins with the growth of the spermatogonia into larger cells known as **primary spermatocytes** (Fig. 201). These are now ready for the first meiotic division, which results in two equal-sized cells, the **secondary spermatocytes.** They in turn undergo division by the second meiotic division to form four equal-sized **spermatids.** The spermatid, a spherical cell with a good deal of cytoplasm, is a mature gamete because it has the haploid number of chromosomes, but, to be a func-

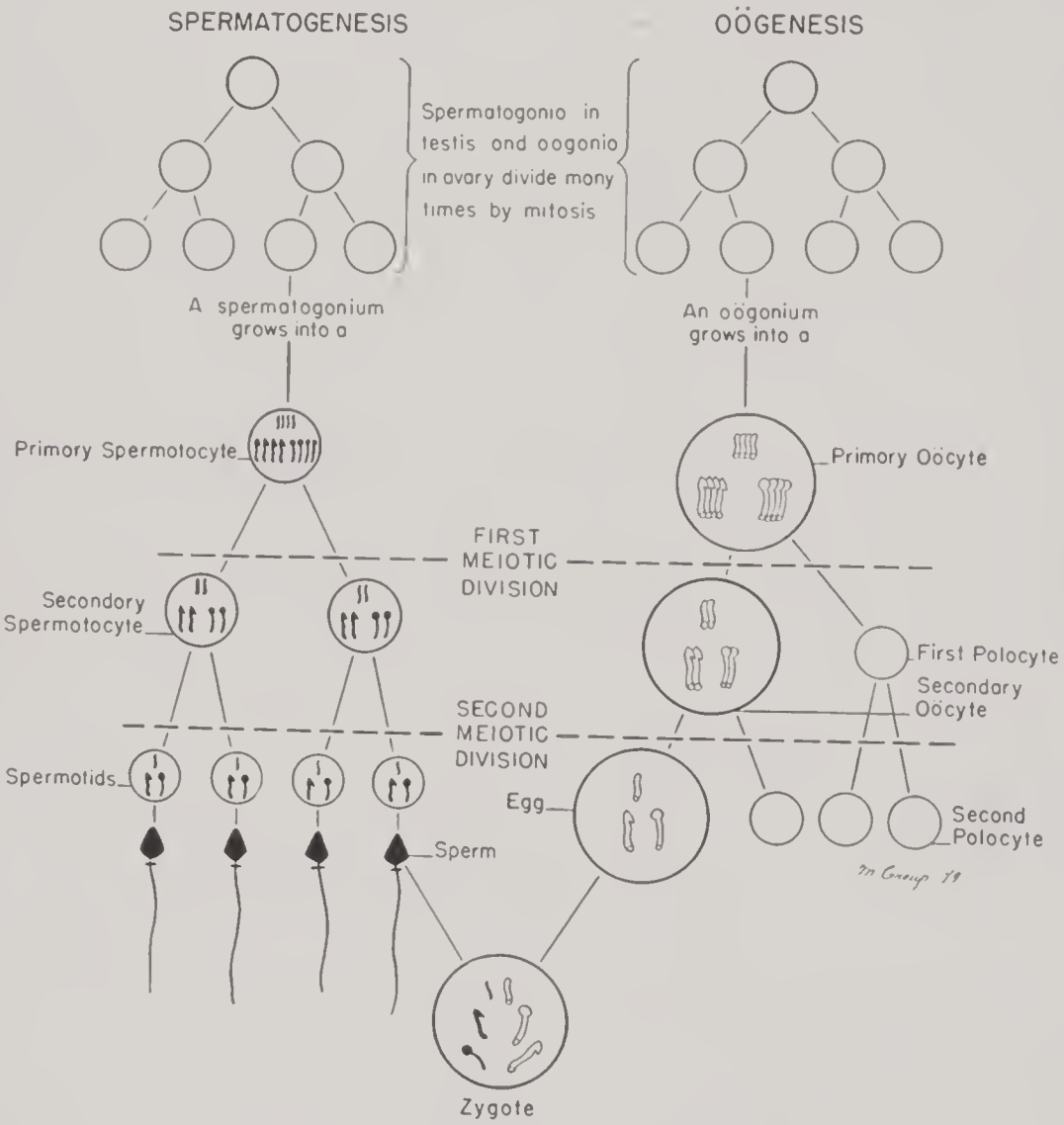


Fig. 201. Comparison of the formation of sperm and eggs.

tional sperm, it must be streamlined for swimming to meet the egg. This requires a complicated process of growth and change (though not cell division). The nucleus shrinks in size and becomes the head of the sperm (Fig. 202), while the sperm sheds most of its cytoplasm. Some of the Golgi bodies from the cytoplasm congregate at the front end of the sperm and form a point which may aid the sperm in puncturing the egg cell membrane. Part of the cytoplasm forms a long, flexible tail which can beat to drive the sperm ahead. The mitochondria move to the point where head and tail meet, and form a small middle piece; this is believed to enable the tail to beat.

The spermatozoa of various animal species may be quite different.

Nearly all sperm have a tail, but there are great variations in its size and shape, as well as in the characteristics of the head and middle piece (Fig. 203). A few animals, such as the parasitic roundworm *Ascaris*, have sperm without a tail, which move by ameboid movement instead. Crabs and lobsters have a curious, tailless sperm with three pointed pro-

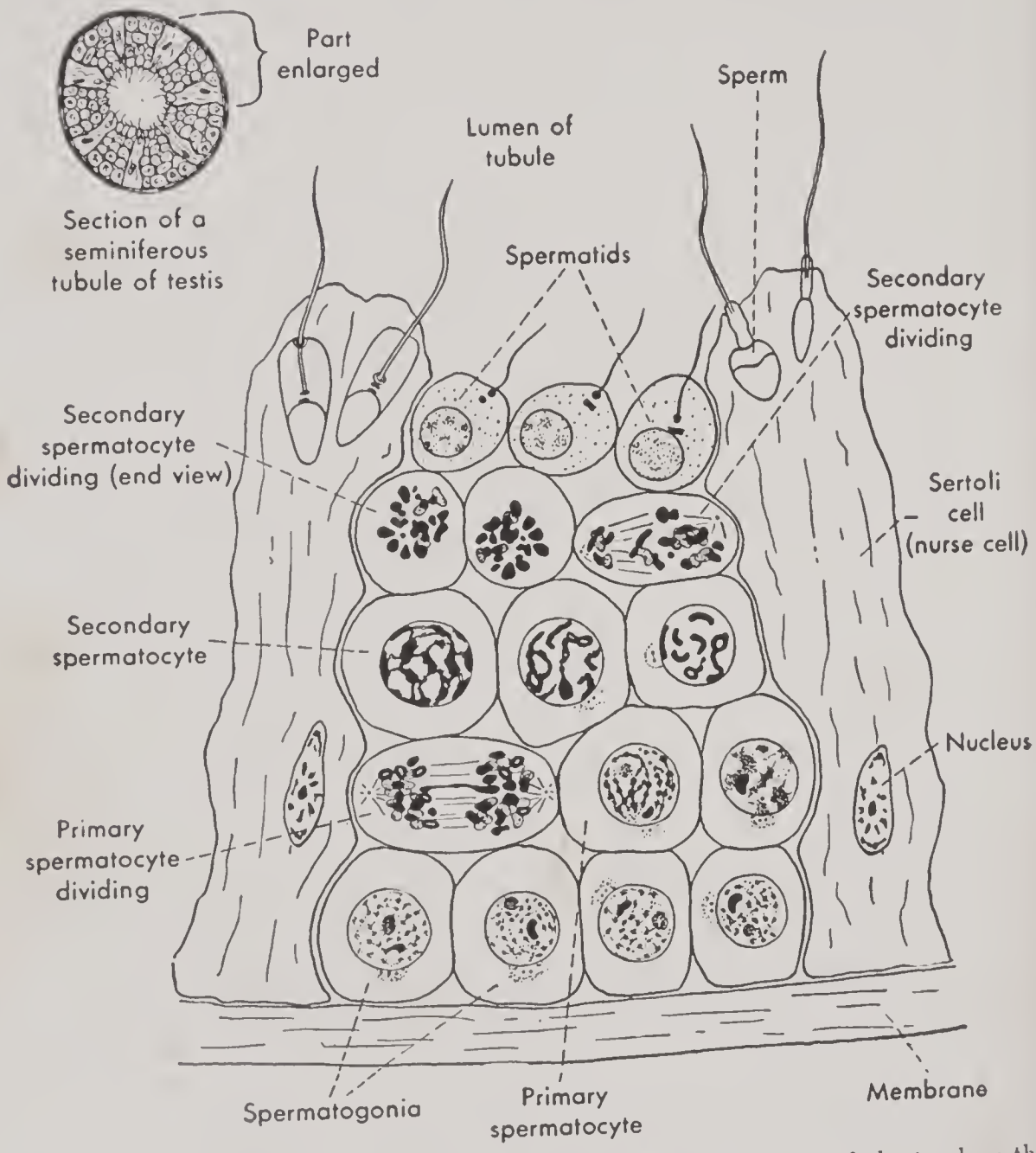


Fig. 202. Diagram of part of a section of the human seminiferous tubule, to show the stages in spermatogenesis and in the transformation of a spermatid into a mature sperm. (Mavor, J. W.: General Biology, The Macmillan Co.)

jections on the head, which stick to the surface of the egg, holding the sperm securely in place. The middle piece uncoils like a spring, and pushes the nucleus of the sperm into the egg cytoplasm, thus accomplishing fertilization.

Oögenesis. The ova or eggs form in the ovary, developing from immature sex cells called **oögonia**. During an organism's early life the oögonia undergo many successive mitotic divisions, just as the spermatogonia do. All these immature cells have the diploid number, of course. At the

time of puberty, in each menstrual month one or more oögonia stop dividing and enter upon a long growth process, eventually to become large cells called **primary oöcytes** (Fig. 201). This growth process lasts much longer in oögenesis than in spermatogenesis, and the primary oöcyte is correspondingly much bigger than the primary spermatocyte. During the process, **yolk** is formed which serves as stored food for development in case the egg is fertilized. At this time many of the "morphogenetic substances" arise which subsequently regulate development in the fertilized egg. At the end of the growth process the primary oöcyte undergoes its first meiotic division. The events occurring in the nucleus —synapsis, the formation of tetrads, and the separation of the homologous chromosomes—are the same as in spermatogenesis, but the division of the cytoplasm is unequal, resulting in one large cell, the **secondary**

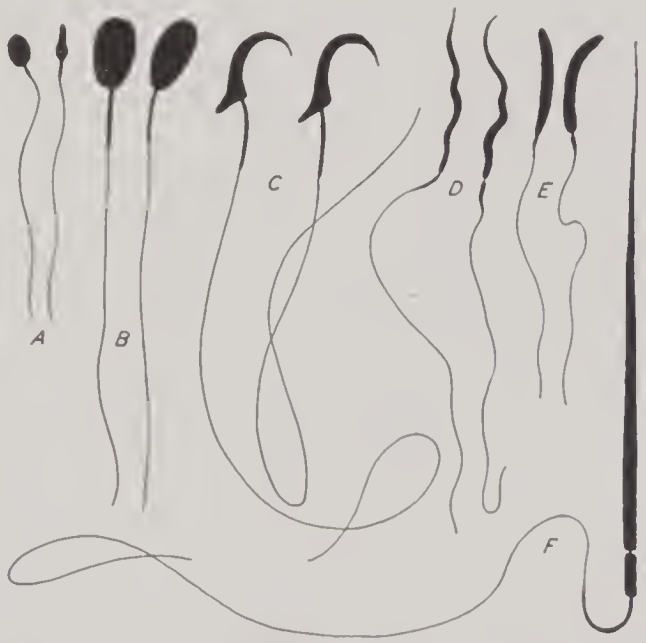


Fig. 203. Spermatozoa from different species of vertebrates, illustrating the differences in size and shape. *A*, Human; *B*, sheep; *C*, rat; *D*, chicken; *E*, frog; *F*, salamander. All are drawn to the same scale. (Turner, C. D.: General Endocrinology.)

oöcyte, which contains the yolk and nearly all the cytoplasm, and one small cell, the first **polocyte,** or polar body, which consists of practically nothing but a nucleus. It was named a polar body before its significance was understood, because it appeared as a small speck at the animal pole of the egg.

In the second meiotic division, the secondary oöcyte again divides unequally into a large **oötid** and a small second polocyte, both of which have the haploid chromosome number. The first polocyte may divide into two additional second polocytes. Now the oötid can grow into a mature ovum. The three small polocytes soon disintegrate, so that each primary oöcyte gives rise to just one ovum, in contrast to the four sperm formed from each primary spermatocyte. The polocytes are necessary to enable the maturing egg to get rid of its excess chromosomes. The unequal cytoplasmic division is necessary to insure that the mature egg will have enough cytoplasm and stored yolk to survive, if fertilized; the primary oöcyte puts all its yolk in one ovum. Thus, the egg has neatly solved the problem of reducing its chromosome number without

losing the cytoplasm and yolk needed for development after fertilization.

The union of a haploid set of chromosomes from the sperm with another haploid set from the egg which occurs in fertilization, reestablishes the diploid chromosome number so that the fertilized egg or zygote, and—by mitosis—all the body cells which develop from it, have the diploid number of chromosomes. Each individual gets exactly half of his chromosomes and half of his genes from his mother and half from his father. Even though an organism may resemble one parent more than the other, both parents have contributed equally to his inheritance. How this can be true will be clear when we consider some of the characteristics of genes.

6. The Genes. The laws of heredity are based on the facts of meiosis and fertilization. Within each chromosome are numerous hereditary factors, each of which differs in some way from all the others. These hereditary units are called **genes,** and each one controls the inheritance of one or more characteristics. Since the chromosomes exist in pairs in the body cells, *each body cell contains two of each kind of gene.* As the chromosomes separate in meiosis and recombine in fertilization, so, of course, the paired genes must separate and recombine. We now know that each chromosome is composed of a linear string of genes, and that the members of a homologous pair of chromosomes have genes arranged in similar order. Thus, if a chromosome has a gene for eye color two thirds of the distance from a given end, its homologous chromosome also will have a gene for eye color two thirds of the distance from that end. Genes for particular traits occur at definite points, called **loci** (singular, *locus*), along the chromosome.

7. Alleles. The mode of inheritance of any given trait can be studied only when there are two contrasting conditions, such as black coat versus brown coat in guinea pigs, or brown eyes versus blue eyes in man. Such contrasting conditions are called **allelomorphs** or **alleles.** Alleles are defined as two contrasting traits, inherited in such a way that an individual may have one but not both of them. It follows that curly and straight hair are alleles, a person having either one or the other. But curly hair and blonde hair are not alleles, because a person may have hair that is both blonde and curly. At the specific locus in the particular chromosome controlling coat color in guinea pigs there may be a gene for brown coat color or a gene for black coat color, but not both. Since there are two homologous chromosomes in body cells and therefore two of each kind of gene, a "pure" black guinea pig (one of a pedigreed race of black guinea pigs) has two genes for black coat—one in each chromosome—and a "pure" brown guinea pig has two genes for brown coat. It is essential to remember that the genes themselves have no color, are neither brown nor black; the brown gene controls certain chemical reactions so that a brown pigment is formed in the hair cells, whereas the black gene alters these chemical reactions, creating black pigment.

In working genetic problems, letters are used as symbols for the genes. A pair of genes for black pigment may be represented by **BB,** and a pair for brown pigment by **bb.** In choosing symbols, a capital letter is used for one gene, and the corresponding lower case letter is used to represent the gene for the contrasting trait or allele.

8. A Monohybrid Cross. If we mate a "pure" brown, male guinea pig with a "pure" black, female guinea pig, the following events occur (Fig. 204): during meiosis in the male the two **bb** genes separate so that each sperm formed has only one **b** gene, and in meiosis in the female the **BB** genes separate so that each ovum has only one **B** gene. Therefore, the fertilization of this egg by a **b** sperm results in an animal with the genetic formula, **Bb**. Since this guinea pig contains both a gene for brown

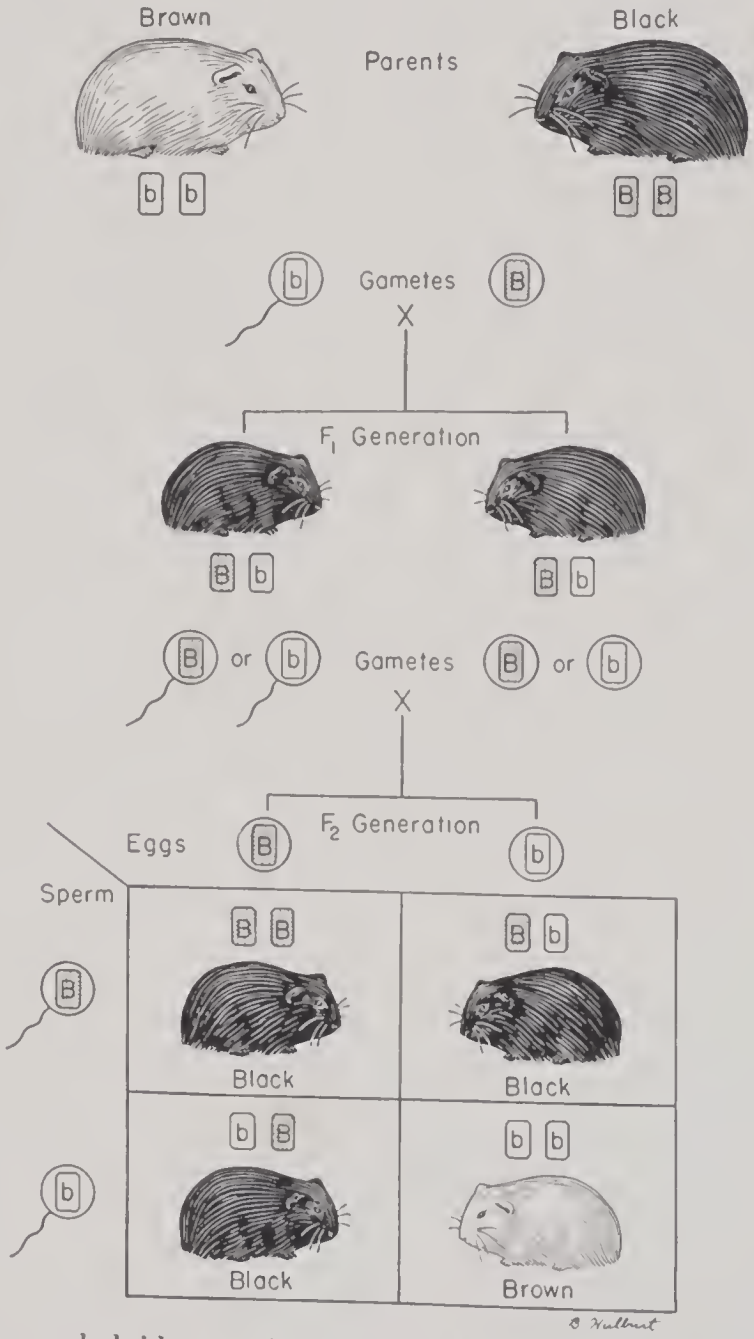


Fig. 204. A monohybrid cross, the mating of a brown with a black guinea pig.

coat and one for black coat, you might expect it to be grey or perhaps spotted; but *it is just as black as its father.* This is because the black gene is **dominant** to the brown gene and produces a black body color even when a brown gene is present. The brown gene is said to be **recessive** to the black one. We may define recessive genes then, as ones which will produce their effects only when an individual has two of them which are identical, and dominant genes as those which will produce their effects even when only one of them is present in an individual. (The dominant gene is given a capital letter and the recessive gene the cor-

responding lower-case letter.) We can now see part of the answer to the apparent contradiction that, although both parents contribute equally to its inheritance, the offspring may resemble one of them more than the other. In one species, black may be dominant to brown, while in another species brown may be dominant to black; the particular condition which obtains in any given form must be determined by experiment.

When an animal or plant has two genes exactly alike, two blacks (**BB**) or two browns (**bb**), it is said to be **homozygous** or "pure" for the character; when it has one dominant and one recessive gene (**Bb**), it is said to be **heterozygous** or **hybrid**. In the cross we have been considering, both the brown and black parents were homozygous for their respective conditions (**BB** or **bb**), and the offspring was heterozygous (**Bb**). Using these terms, we can now formulate better definitions for dominant and recessive: a recessive gene is one which will produce its effect only when homozygous; a dominant gene is one which will produce its effect whether it is homozygous or heterozygous.

If two of the heterozygous black guinea pigs from the aforementioned cross are mated, the following events occur: in meiosis, the chromosome containing the **B** gene first synapses with and then separates from the chromosome containing the **b** gene, so that each sperm or egg has either a **B** gene or a **b** gene, but never both. Sperm and eggs containing **B** genes and those with **b** genes are formed in equal numbers. Since there are two types of eggs and two types of sperm, four combinations in fertilization are possible, and these occur in equal numbers. There is neither any special attraction nor repulsion between an egg and sperm containing the same genes: a **B** egg is just as likely to be fertilized by a **B** sperm as by a **b** sperm.

To see at a glance the possible zygote combinations, a "checkerboard" is made up, in which the possible types of eggs are represented along the top, the possible types of sperm are indicated along the left side, and the squares are filled in, showing the possible zygote combinations (Fig. 204). Three fourths of all the offspring will be **BB** or **Bb**, and therefore black, and one fourth will be **bb**, and appear brown. This 3 to 1 ratio is characteristic of the second generation offspring of a cross of two individuals which differ in a single trait governed by a single pair of genes. The generation with which a particular experiment is begun is called the P_1, or **parental generation**. Offspring of this generation are called the F_1, or **first filial generation**. Those resulting when two F_1 individuals are bred constitute the F_2, or **second filial generation** (grandchildren); those from mating of two F_2 individuals make up the F_3 generation, and so on.

9. Phenotype and Genotype. The appearance of an individual with respect to a certain trait is known as its **phenotype**, while the organism's genetic constitution is called its **genotype**. The phenotypic ratio of the cross we have been discussing is 3 black: 1 brown, and the genotypic ratio is **1 BB: 2 Bb: 1 bb**. The phenotype may be defined as the external appearance of a given trait expressed in words such as black, brown, and so on. The genotype may be defined as the genetic constitution of an individual expressed in symbols, such as **BB**, **Bb** or **bb**. Guinea pigs which are **BB**

and **Bb** are alike phenotypieally, that is, both *appear* black, but they differ genotypieally. The genotypes could be determined only by breeding tests. It is also possible for organisms to have like genotypes but different phenotypes.

It is important to realize that *all genetic ratios are probability ratios.* This means that if two heterozygous black guinea pigs are bred and produce exactly four offspring, although it is *probable* that three will be black and one brown, all *might* be black, or all might be brown, though the latter possibility would rarely occur. Or, the combinations of 3 blacks: 1 brown; 2 blacks: 2 brown; or 1 black: 3 brown also might occur. If 100 such matings were made, however, approximately 300 of the offspring would be black and 100 would be brown. The ratio of black to brown approaches more and more closely to an exact 3:1 as larger numbers of offspring are produced. This probability ratio can be stated another way: in mating two heterozygous individuals, (**Bb**), there are three chances out of four that any *particular* offspring will show the dominant character, and one chance out of four that it will show the recessive character.

In man, eye color is inherited by a pair of genes, brown eye color (**B**) being dominant to blue (**b**). If two heterozygous, brown-eyed people mate, there are three chances out of four that their child will have brown eyes, and one chance out of four that it will have blue eyes. Each mating is a separate, independent event, not affected by the results of previous matings. Thus, if these two heterozygous, brown-eyed parents have three brown-eyed children and are expecting a fourth child, the fourth one, too, has three chances out of four of being brown-eyed, and only one chance out of four of having blue eyes.

10. Mendel's First Law. The mating of black and brown guinea pigs previously described illustrates Mendel's First Law, sometimes called the "Law of the Purity of Gametes" or the Law of Segregation. This may be stated as follows: genes exist in individuals in pairs, and in the formation of the gametes, each gene separates or segregates from the other member of the pair and passes into a different gamete, with the result that each gamete has one and only one of each kind of gene. In the guinea pig problem, the brown gene is unaffected by the black gene when it exists in the heterozygous black guinea pig with it, but it segregates from the black gene, passes into the next generation, and may produce a brown guinea pig.

11. Test Crosses. In the F_2 of the black-brown guinea pig mating, we found a ratio of three black: 1 brown guinea pig. Although the black guinea pigs are alike phenotypically, they differ genotypically. One third of them are homozygous black (**BB**); the other two thirds are heterozygous black (**Bb**). These can be differentiated by a breeding test, the "test cross" or "back cross." To perform the test, each black guinea pig is bred with a homozygous recessive (brown) one (Fig. 205). If all the offspring are black, the parent being tested is homozygous (**BB**), and if any of the offspring are brown, the parent is heterozygous (**Bb**).

This sort of testing is of the greatest importance in the commercial breeding of animals or plants, where the breeder is trying to establish a

strain which will "breed pure" for a certain character. Formerly, farmers and stock breeders could pick only what appeared to be the best animals for breeding stock, or what seemed to be the best plants in a field, to bear the seed for the next year's crop. This selection by phenotype alone was not very successful because it was not based on knowledge of which animals and plants were homozygous and which heterozygous. As a result, the heterozygous individuals continued to bear some offspring with the less desirable qualities.

The more modern method of breeding, **progeny selection,** is one by which a breeder, in effect, tests the genotypes of his breeding stock by making matings and observing the offspring. If these are superior in

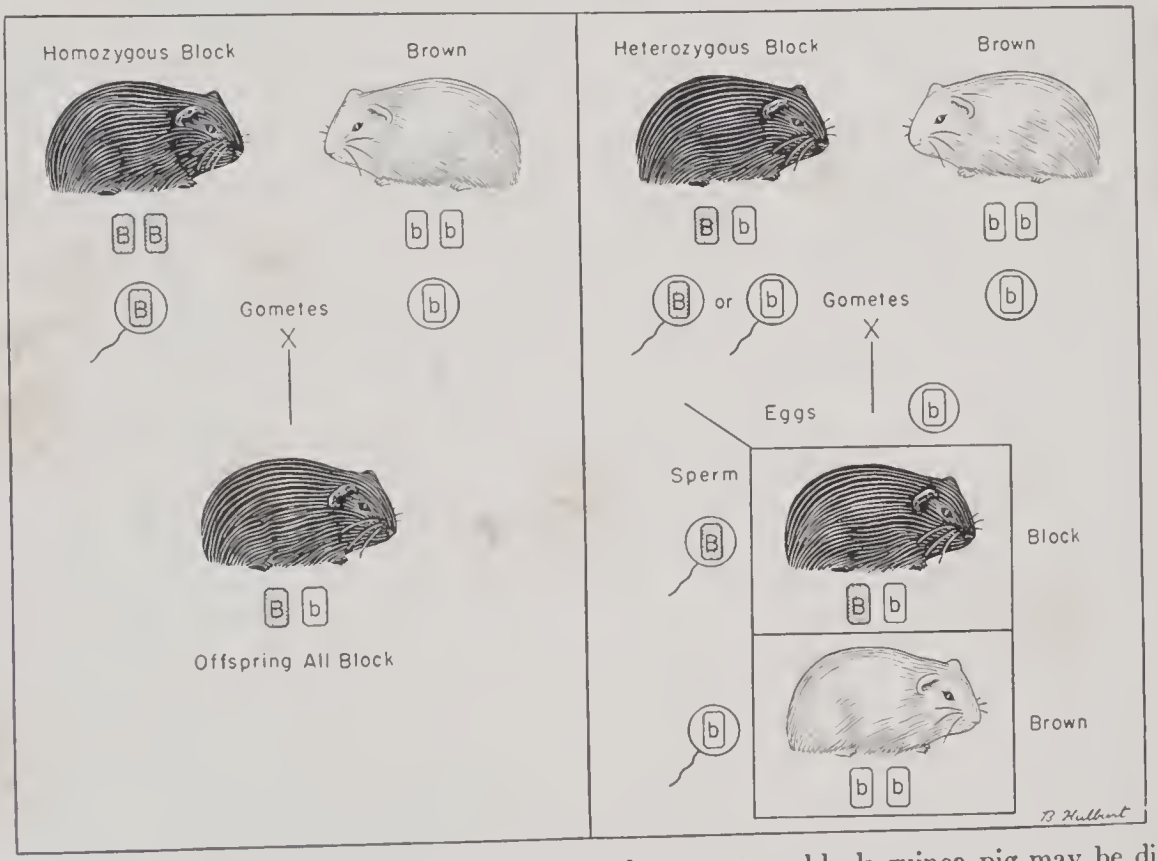


Fig. 205. Diagram of test crosses, whereby a heterozygous black guinea pig may be distinguished from a homozygous black one. If a homozygous black is mated with a brown one (left), all of its offspring are black. If a heterozygous black is mated with a brown (right), half of the offspring are black, and half brown.

respect to the desirable trait, the parents are thereafter used regularly for breeding. Two bulls may both look healthy and vigorous, yet one will have daughters with superior milk production and the other will not. By observing the progeny, and using regularly for breeding only those animals that produce superior offspring, the desirable qualities of a strain of animals can be increased rapidly. The method of progeny selection enabled one geneticist to raise the average annual egg production of a flock of hens from 114 to 200 eggs, in eight years. Of course, for successful progeny selection, careful pedigrees must be kept.

12. Incomplete Dominance. In some species one gene is not completely dominant to the other, heterozygotes being intermediate between the two parents. This condition, known as **incomplete dominance,** is in sharp contrast to the complete dominance of black over brown in the

guinea pig cross. In sweet peas, for instance, the offspring of a cross of a red-flowered plant with a white-flowered plant all have pink flowers. When two pink-flowered plants are crossed, the offspring are one fourth red, one half pink, and one fourth white. In such crosses the phenotypic and genotypic ratios are identical. In cattle and horses, red coat color is incompletely dominant to white, the heterozygote being roan.

13. Deducing Genotypes. Another type of problem which a knowledge of genetics enables us to solve is that of deducing the genotypes of parents (and from that the probable character of additional offspring) from the results of a particular cross. In chickens, for example, the gene

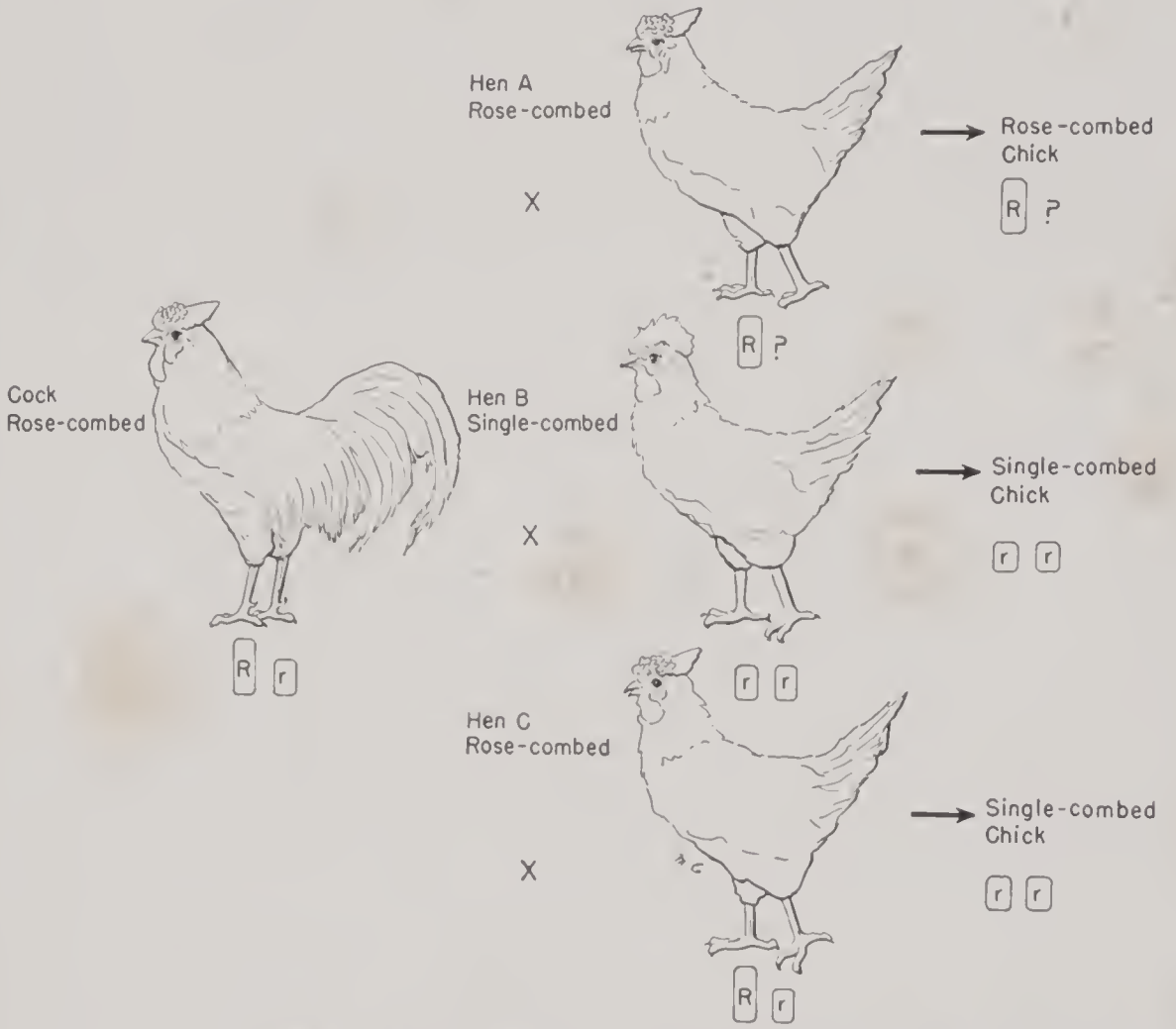


Fig. 206. Deducing the parental genotypes from the phenotypes of the offspring. See text for discussion.

for rose comb (**R**) is dominant to the gene for single comb (**r**). Suppose that a cock is mated to three different hens (Fig. 206): the cock and hens A and C have rose combs; hen B has a single comb. Breeding the cock with hen A produces a rose-combed chick; with hen B, a single-combed chick; and with hen C, a single-combed chick: What offspring can be expected from further matings of the cock with these hens?

Since the single-combed condition is recessive, all the hens and chicks phenotypically single-combed must be homozygous. We can deduce, then, that hen B and the offspring of hens B and C are genotypically **rr**. All those phenotypically rose-combed have at least one **R** gene, and the cock, and hens A and C, are therefore R?. The fact that the offspring of the cock and hen B was single-combed proves that the cock

is heterozygous. The single-combed chick received one **r** gene from its mother, but must have received the other from its father. The fact that the offspring of the cock and hen C had a single comb proves that hen C also was heterozygous. We now know the genotypes of all the individuals concerned except hen A, and it is impossible to decide from the data given whether she is homozygous or heterozygous. Further breeding would be necessary to determine this. Additional matings of the cock with hen B would result in one half rose-combed: one half-single-combed individuals; additional mating with hen C would produce three fourths rose-combed: one fourth single-combed chicks.

The science of genetics resembles mathematics in that it consists of a few basic principles which, once grasped, enable the student to solve a wide variety of problems. Let us summarize the fundamental concepts. Inheritance is biparental: both parents contribute to the genetic constitution of the offspring. Genes are not altered by existing together in a heterozygote. Genes must be single in a gamete; either one or the other, but never both of a pair of genes is present. The gametes mate at random, irrespective of the genes they contain, and a sperm containing a **B** gene is equally likely to fertilize a **B** or a **b** egg; there is no specific attraction or repulsion between a **B**-containing egg and a **B**-containing sperm.

In working genetics problems, it is well to follow the procedure given here, in order to avoid errors:

1. Write down the symbols you are using for each gene.
2. Determine the genotypes of the parents, deducing them from the phenotypes of the offspring, if necessary.
3. Derive all possible kinds of gametes from these genotypes.
4. Set up a "checkerboard," putting all the possible types of sperm along the side and all the possible kinds of eggs along the top.
5. Fill in the checkerboard and read off the genotypic and phenotypic ratios among the offspring.

QUESTIONS

1. What is the difference between heredity and genetics?
2. What are the two main causes of variations in living things?
3. What is accomplished by mitosis? By meiosis?
4. What is a chromosome? Describe its structure.
5. In a human cell undergoing mitosis, how many chromosomes are present in the metaphase? In the anaphase? In the resting daughter cell?
6. Outline briefly the events occurring in each stage of mitosis.
7. Discuss the physical conditions which cause mitosis to occur.
8. Compare mitosis with meiosis.
9. Compare spermatogenesis with oögenesis.
10. In an animal with a haploid number of 10, how many chromosomes are present in a spermatogonium? In the tetrad stage? In the anaphase of the first meiotic division? In the metaphase of the second meiotic division? In a first polocyte? In a second polyocyte?
11. If a particular character in a certain species of animal were always transmitted from the mother to the offspring, but never from the father to the offspring, what would you conclude about the method of its inheritance?
12. How many human sperm will be produced from 100 primary spermatocytes? How many eggs will be produced from 100 primary oöcytes?
13. What do the following genetic symbols mean: **A, a, AA, aa, Aa?**

14. Define the following: gene, locus, allelomorph, dominant, recessive, homozygous, heterozygous, phenotype, genotype, back-cross.

15. In peas, yellow color is dominant to green. What will be the offspring of homozygous yellow x green? heterozygous yellow x green? heterozygous yellow x homozygous yellow? heterozygous yellow x heterozygous yellow?

16. Could two blue-eyed parents have a brown-eyed child? Could two brown-eyed parents have a blue-eyed child?

17. If two animals heterozygous for a single pair of genes are crossed and there are 200 offspring, about how many will have the dominant phenotype?

18. When two long-winged flies were mated, the offspring included 77 with long wings and 24 with short wings. Is the short-winged condition dominant or recessive? What are the genotypes of the parents?

19. A blue-eyed man, whose parents were brown-eyed, marries a brown-eyed woman whose father was blue-eyed and whose mother was brown-eyed. This couple have a blue-eyed child. What are the genotypes of all the individuals mentioned?

20. Outline a breeding procedure whereby a true-breeding strain of red cattle could be established from a roan bull and a white cow.

SUPPLEMENTARY READINGS

Colin, E. C.: *Elements of Genetics.* 2d ed. Philadelphia, The Blakiston Company, 1945.
An elementary discussion of the principles of heredity, with a good, readable discussion of human genetics.

Snyder, L. H.: *The Principles of Heredity.* 3rd ed. Boston, D. C. Heath & Co., 1946.
A clearly written introduction to genetics.

CHAPTER 24

GENETICS

I. MENDEL'S SECOND LAW

THE TYPE of genetic mating discussed in the previous chapter, where only one pair of genes is considered, is called a **monohybrid cross.** For the sake of simplicity it is best to begin the study of genetics with such a problem, but it is often necessary for the geneticist to consider the simultaneous inheritance of two, three, or even more pairs of genes. Such crosses are called **dihybrid, trihybrid,** and so on. Problems involving dihybrid or trihybrid crosses are solved exactly as are problems involving monohybrid crosses, the only difference lying in the greater number of types of gametes and the consequently greater possible number of different zygotes.

When two pairs of genes lie in different (nonhomologous) chromosomes, *each pair of genes is inherited independently of the other pair;* that is, each pair separates during meiosis independently of the other. In writing the genetic formula of an organism in which we are considering two pairs of genes, we must write two of each kind of symbol. Thus, a black, short-haired guinea pig has the symbol **BBSS** (short hair being dominant to long hair) and a brown, long-haired one has the symbol **bbss.** The gametes of the **BBSS** animal are all **BS.** Those of the **bbss** guinea pig are all **bs.** Now let us suppose that the **B-b** genes are located in a rod-shaped chromosome, and the **S-s** genes in a hooked chromosome. During meiosis, the respective homologous chromosomes synapse and then separate so that each gamete gets one and only one of each kind. Since both parents are homozygous all the gametes produced by each are identical. All the offspring, therefore, are **BbSs,** heterozygous for hair color and for hair length, and all are phenotypically black and short-haired.

Each of these F_1 individuals produces *four* kinds of gametes in equal numbers—**BS, Bs, bS** and **bs**—so that when two of them are mated, sixteen combinations are possible in the F_2 generation (see checkerboard, Fig. 207). Adding them together, there are nine black, short: three black, long: three brown, short: one brown, long. *This 9:3:3:1 ratio is characteristic of the second generation of a cross of two individuals differing in two characters whose genes are located in nonhomologous chromosomes.* Keep in mind that this is a *probability* ratio, which means that there are nine chances out of sixteen that any particular offspring will be black and short-haired, and only one chance out of sixteen that it will be brown and long-haired. A great many crosses probably would have to be made before the results would approach this theoretical ratio closely. This ratio illustrates Mendel's Second Law, the Law of Independent Segregation, which states that the members of one pair of genes separate (segregate) from each other in meiosis independently of the

members of other pairs of genes and come to be assorted at random in the resulting gametes.

In a similar fashion, problems involving three different pairs of genes may be solved. Of course, in a trihybrid cross the three heterozygous pairs of genes form *eight* types of gametes in equal numbers, and the

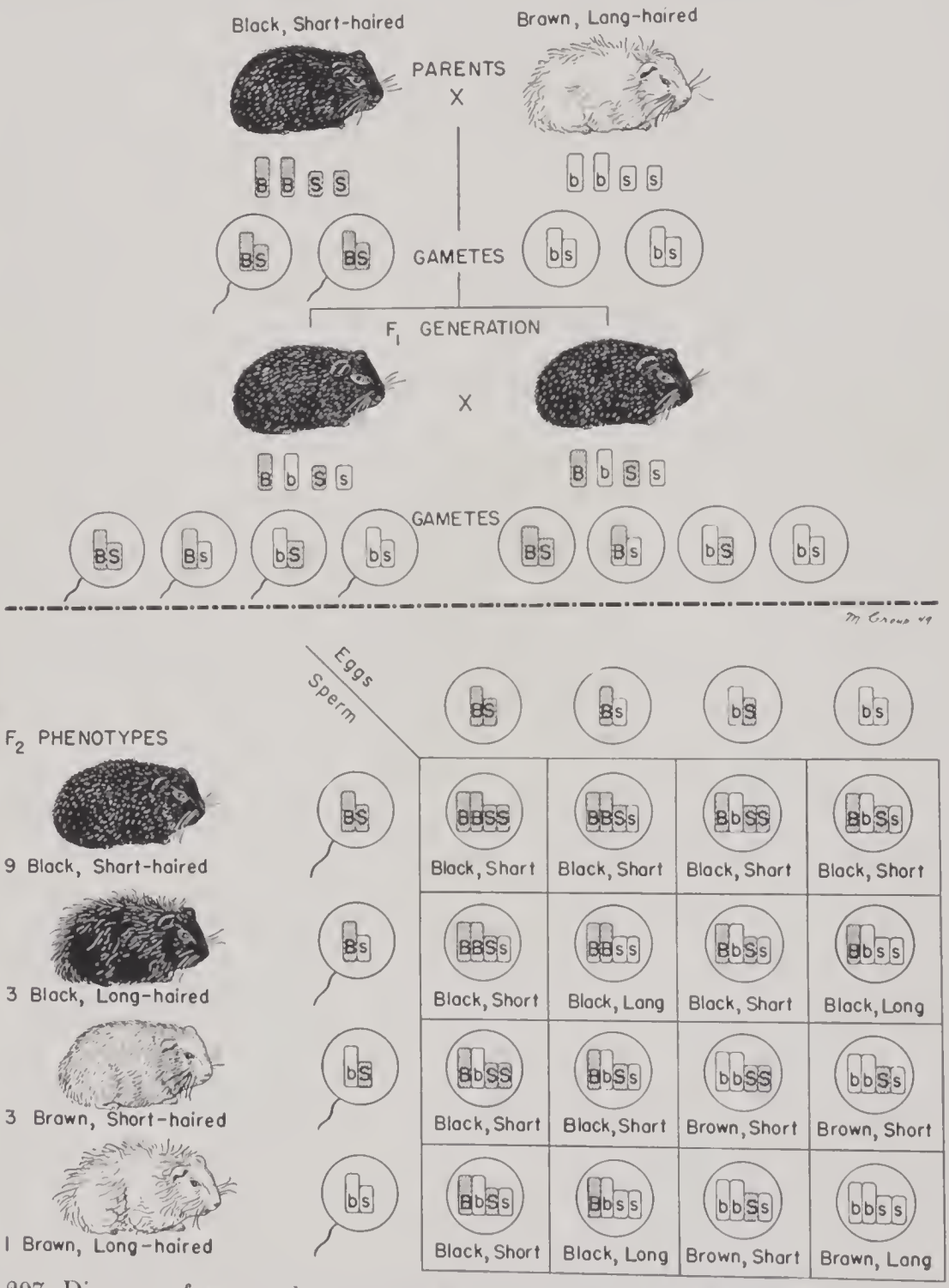


Fig. 207. Diagram of a cross between a black, short-haired guinea pig and a brown, long-haired one, illustrating independent assortment.

union of these gives sixty-four possible zygotes in the F_2 generation. In peas, yellow (**Y**) seed color is dominant to green (**y**), smooth (**S**) seeds are dominant to wrinkled (**s**), and tall plants (**T**) are dominant to dwarf (**t**). A cross of a homozygous yellow, smooth, tall (**YYSSTT**) with a homozygous green, wrinkled, dwarf (**yysstt**) produces offspring all of which are yellow, smooth and tall (**YySsTt**). When two of these F_1

plants are mated, F_2 offspring are produced in the ratio of twenty-seven yellow, smooth, tall: nine yellow, smooth, dwarf: nine yellow, wrinkled, tall: nine green, smooth, tall: three yellow, wrinkled, dwarf: three green, wrinkled, tall: three green, smooth, dwarf: one green, wrinkled, dwarf. Work out the checkerboard to prove this.

II. INTERACTIONS OF GENES

So far, we have considered situations in which there is a simple relationship between gene and character, each gene producing a single trait. In reality, as genetic research soon showed, this is not always the case. The study of inheritance is complicated by the fact that two or more pairs of genes may interact in any one of several ways to produce a single trait. One of the simpler types of interaction is illustrated by the inheritance of combs in poultry. We mentioned previously that the gene for rose comb (**R**) is dominant to that for single comb (**r**). Another pair of genes governs the inheritance of pea comb (**P**) versus single comb (**p**). The genotype of a single-combed fowl, then, must be **pprr**; a pea-combed fowl is either **PPrr** or **Pprr**; and a rose-combed fowl is either **ppRR** or **ppRr** (Fig. 208). Investigators found that when a homozygous, pea-combed fowl is mated to a homozygous, rose-combed one, the offspring have neither pea nor rose combs, but a completely different type called walnut comb. Therefore, the walnut-combed condition is produced whenever a fowl has one or two **R** genes plus one or two **P** genes, and the genotypes **PPRR, PpRR, PPRr,** and **PpRr,** are all phenotypically walnut-combed. When two heterozygous, walnut-combed fowls are mated, offspring in the ratio of nine walnut: three rose: three pea: one single are produced. Make a checkerboard to demonstrate this.

1. Complementary Genes. It sometimes happens that two pairs of independent genes are related to each other in such a way that neither dominant can produce its effect unless the other is present. Such pairs of genes are called complementary genes. The presence of both dominants produces one character; the alternate character is produced by the absence of either one or both. An example will make this clear. A geneticist was amazed one time when crossing two white races of sweet peas to find all the offspring purple! Crossing two of the F_1 purple plants produced an F_2 generation in the ratio of nine purple: seven white (Fig. 209). Two pairs of factors proved to be involved: one gene (**C**) produced a white raw material from which a purple pigment could be made by an enzyme produced by the second gene (**E**). The homozygous recessive (**cc**) caused the absence of the raw material, and the recessive (**ee**) caused the absence of the enzyme, either of which, of course, prevented the formation of the purple pigment. In this particular cross, one of the races of white sweet peas lacked the raw material gene, being genotypically **ccEE**, the other lacked the enzyme gene and was genotypically **CCee**. Mating **ccEE** with **CCee** resulted in F_1 offspring all of which were **CcEe**—phenotypically purple—because both the raw material and the enzyme were present. When these F_1 purple plants were mated, purple and white plants appeared in the F_2 generation, in the ratio of 9:7. Nine out of sixteen had at least one **C** and one **E** and were purple; seven out of the sixteen lacked either a **C** or an **E** (or both) and were

white. This 9:7 ratio is characteristic of the F_2 generation of a cross involving complementary genes. A race of sweet peas breeding true for purple could be set up by selecting two **CCEE** plants and mating them.

2. Supplementary Genes. A slightly different sort of interrelationship between genetic factors is demonstrated by supplementary genes. These are two independent pairs which interact in such a way that one dominant will produce its effect whether the other is present or not, but

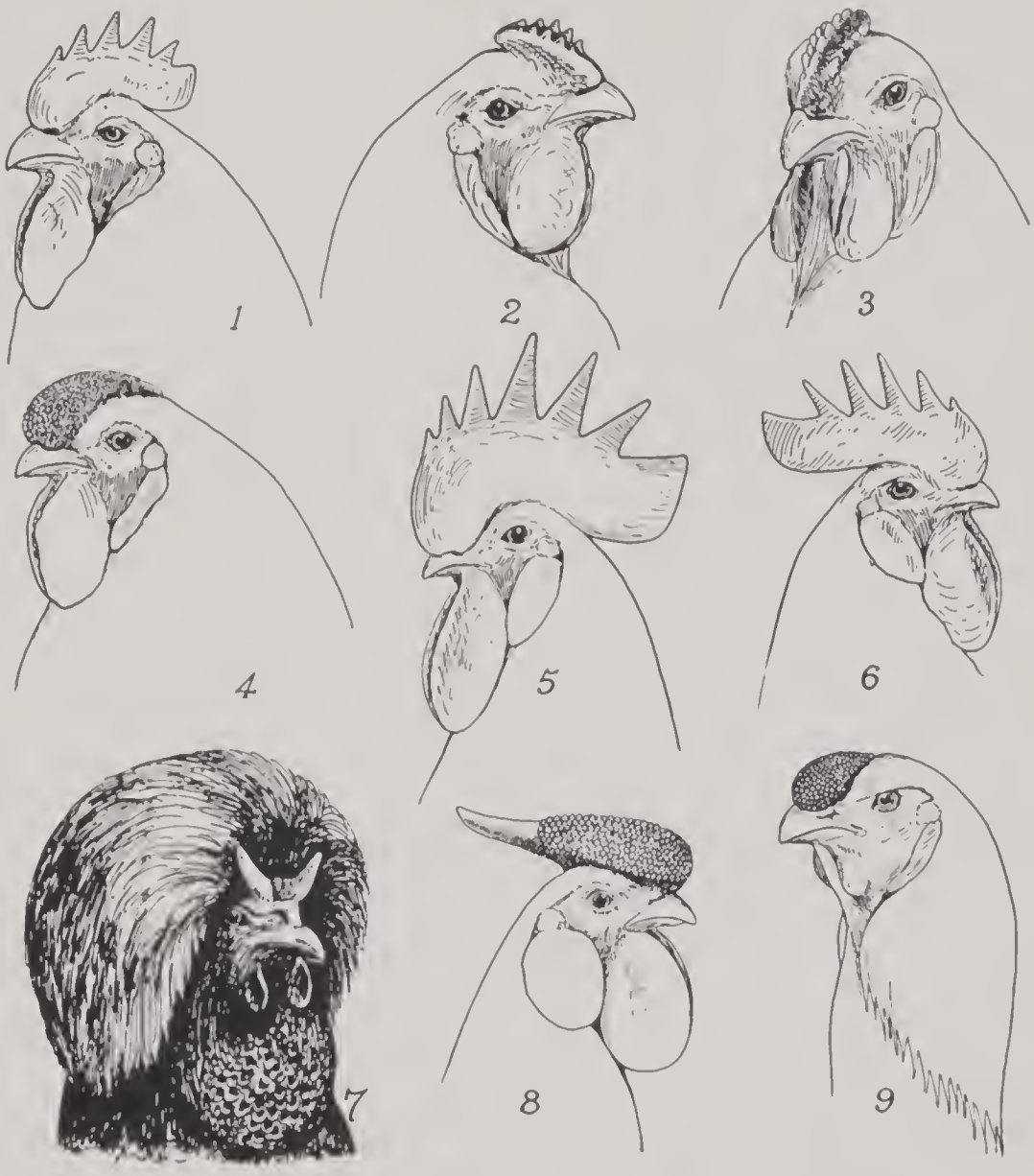


Fig. 208. Heads of roosters, showing the different types of genetically determined combs. *1*, *5*, and *6*, Single combs; *2* and *3*, pea combs; *4* and *8*, rose combs; *7*, V-shaped; *9*, strawberry. (Courtesy of the United States Department of Agriculture.)

the second can produce its effect only in the presence of the first. The inheritance of coat color in guinea pigs supplies us with an example of supplementary genes. In addition to the **B** gene for black coat and the **b** gene for brown coat mentioned previously, there is a gene, **C**, which is necessary for the production of any pigment at all in the coat; the homozygous recessive **cc** produces the albino condition (complete absence of pigment in hair and eyes). Because of this, mating an albino of the genotype **ccBB** with a brown guinea pig, **CCbb**, will produce an F_1 generation all of which are black! They will have the genotype **CcBb**,

and when two such animals are crossed, their offspring will be in the ratio of nine black: three brown: four albino. Make a checkerboard to show this. This 9:3:4 ratio is characteristic of the F_2 generation in

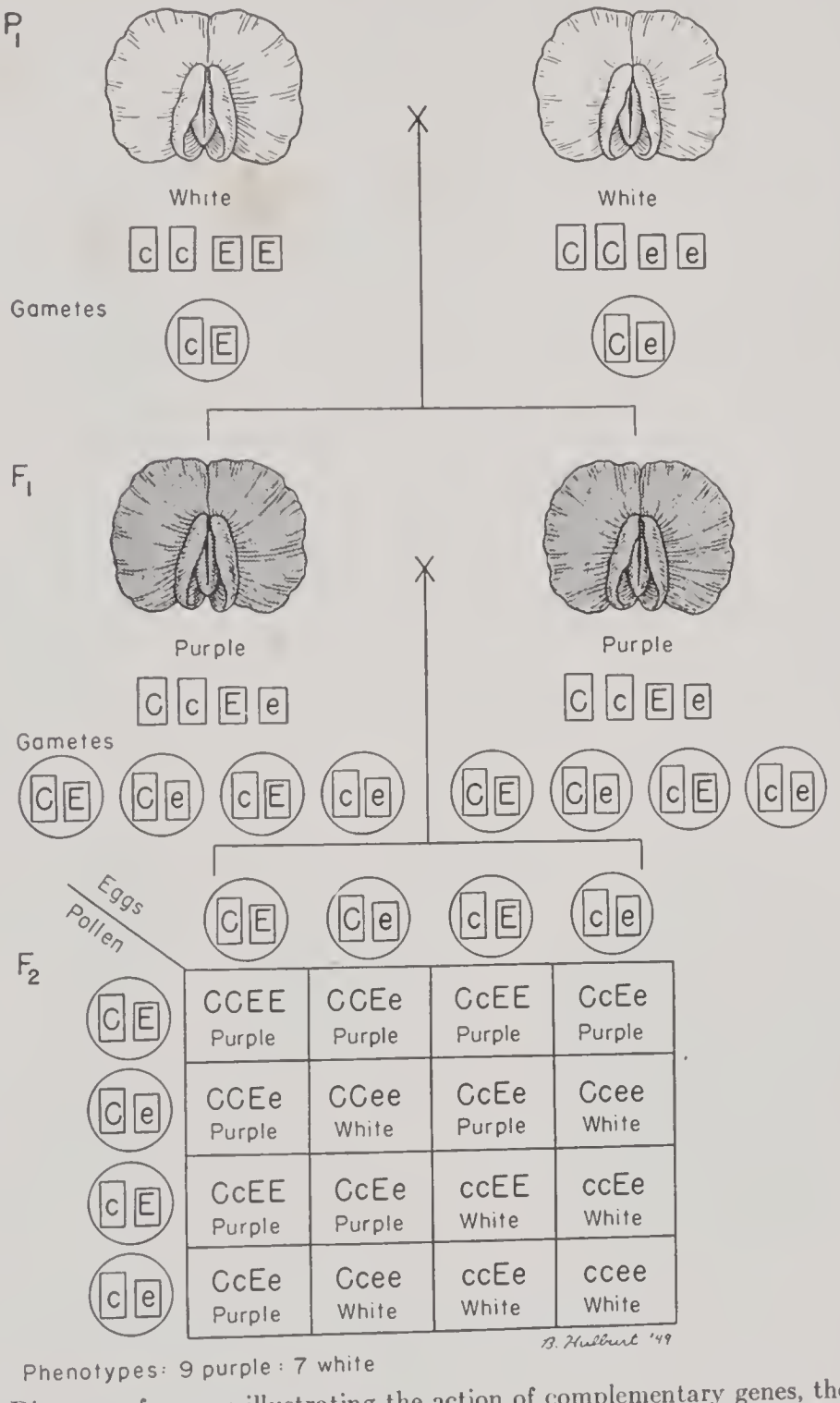


Fig. 209. Diagram of a cross illustrating the action of complementary genes, the two pairs of genes which regulate flower color in sweet peas. Note that for a colored flower, the plant must have at least one C and one E.

a cross involving supplementary factors. The color gene (**C**) will produce its effect no matter which of the **B-b** genes is present, but the **B** or **b** gene can produce its effect only when at least one **C** is present.

It is possible for both complementary and supplementary genes to be involved in one cross. In maize, for example, there are **C** and **R** genes necessary for red kernels, the absence of either causing white kernels.

Hence they are complementary genes. In addition, there is a **P** gene which produces purple kernels, but only if both a **C** and an **R** are present. This, then, is supplementary to the other two pairs of genes.

It is beyond the scope of this book to discuss further complexities of gene interraction. The problems indicated here are the simplest with which the geneticist deals, and most traits are governed by a multitude of genes which interact with each other and with the environment to produce the final phenotype. The unscrambling of these interactions provides the gencticist with many difficult problems. Dr. W. E. Castle, of Harvard University, has found that more than twelve pairs of genes interact in various ways to produce just the coat color of rabbits, and the many geneticists working with fruit flies have found that over 100 genes are concerned with the color and shape of the eyes.

3. Multiple Factors. The principles of heredity that we have discussed underlie the inheritance of practieally all traits in both plants and animals. But not all characters are inherited in this simple fashion; in fact, most of the characters such as height, weight, intelligence, and skin color in man, as well as such commercially important factors as milk production in cows, and egg production in chickens, are inherited in a complex way sometimes called **blended inheritance.** In this, the offspring are intermediate between the parents. Thus, the children of a Negro-white mating are all mulattoes, with skin colors intermediate between those of their parents. Blended inheritance is controlled by **multiple factors,** *two or more independent pairs of genes which affect the same character in the same way and in an additive fashion.* The investigation of the inheritance of skin color was pursued by Davenport in Jamaica, where there is no "color line" and matings between Negro and white occur freely. He found that two pairs of genes are involved, which he called **A-a** and **B-b.** The capital letters stand for genes causing dark skin—the more capital letters, the darker the skin. That is, the genes affect the character in an additive fashion. A full Negro has all four dominant genes **AABB** (the genes are incompletely dominant, of course), and a white has all four recessive genes, **aabb.** The F_1 offspring of a mating of **aabb** with **AABB** are all **AaBb** and have intermediate (mulatto) skin color. A mating of two such mulattoes produces a wide variety of skin color in the offspring, ranging from as dark as the original Negro parent to as white as the original white parent (Table 10). Multiple-factor crosses are characterized by producing an F_1 generation intermediate between the two parents and showing little variation, and an F_2 generation showing a wide variation between the two parental types, but with a greater number of the intermediate forms, and only a few as extreme as either grandparent. Of the sixteen possible zygote combinations from a cross of **AaBb** with **AaBb** only one **(AABB)** will be as dark as the Negro grandparent, and only one (**aabb**) will be as light as the white grandparent. Since the genes **A** and **B** produce about the same amount of darkening of the skin, the genotypes **AaBb, AAbb** and **aaBB** all produce the same phenotype, mulatto. The genotype of a given mulatto can be determined only by observing his offspring.

Skin color in man is rather a simple example of multiple-factor inheritance, because only two pairs of genes are involved. Height in man

is inherited by a much more complex set of multiple factors, possibly ten or more pairs of genes being involved. Since tallness is recessive to shortness, the more capital letters in the genotype, the shorter the individual. Because of the many pairs of genes involved and because height is modified by environmental conditions, we do not have the alternative conditions, short versus tall, or even short, medium and tall. Instead, there are people of every height from about 55 inches to about 84 inches. If we measured the heights of a thousand American adults taken at random, we would find the majority of average height—perhaps 68 inches—and only a few as tall as 80 inches, or as short as 55. In a diagram, when the number of people of each height is plotted against the height in inches, and the points connected, the result is a bell-shaped curve, called a "normal curve" or curve of normal distribution.

Table 10. Multiple Factor Inheritance of Skin and Color in Man

Parents	AaBb (Mulatto)	×	AaBb (Mulatto)						
Gametes	AB	Ab	aB	ab		AB	Ab	aB	ab

Offspring:

1 with 4 dominants—AABB—phenotypically Negro
4 with 3 dominants—2 AaBB and 2 AABb—phenotypically "dark"
6 with 2 dominants—4 AaBb, 1 AAbb, 1aaBB—phenotypically mulatto
4 with 1 dominant —2 Aabb, 2 aaBb—phenotypically "light"
1 with no dominants—aabb—phenotypically white

All living things vary, and their variations usually follow this normal curve. If you pick up 1000 seashells of the same species and measure their length, or count the number of kernels on 1000 ears of corn, or the number of pigs per litter in 1000 litters, or weigh 1000 hen's eggs, you will find the normal curve in each case. The variation resulting in this distribution may be caused by hereditary differences, by environmental differences or by a combination of the two. Commercial breeders who are trying to breed cows that will give more milk, or hens that will lay bigger eggs, or ears of corn with more kernels per ear, are working with multiple factors. By selecting organisms which approach the phenotype they are seeking, and using them in further matings, they gradually produce true breeding strains with the commercially desirable trait; that is, they select a strain homozygous for all the dominant (or recessive) factors involved. It is evident that there is a limit to the effectiveness of breeding by selection. When the strain becomes homozygous for all the factors involved, further selective breeding cannot increase the desirable quality.

Multiple factors sometimes affect a character, the presence or absence of which is determined by a single pair of genes. In most mammals which have been tested, the presence or absence of spots in the coat is determined by a single pair of factors. The gene for the presence of spots (**s**) is recessive to the gene for solid color (**S**). The size and distribution of the spots varies widely among different animals. It is possible, by selective breeding, to produce animals with more or fewer spots, which shows that hereditary factors, and not prenatal environment, are mainly responsible for the amount of spotting. The type of

inheritance involved is characteristic of multiple factors: the F_1 is intermediate between the two parents; the F_2 is variable, including some individuals with as many spots as one grandparent and some with as few as the other. The term **modifying factors** is applied to multiple factors which affect the *degree* of expression of another gene. Many examples of such factors are known.

4. Multiple Alleles. In our previous discussion we have considered only genes which exist in pairs, one dominant and one recessive. Many genes, however, have more than one allele: in addition to a dominant and a recessive gene, there may be one or more intermediate genes forming a series. Multiple alleles are three or more conditions of a single locus, producing different phenotypes. Among the members of a species, the alleles are inherited in such a way that a particular individual receives any two of the genes and never more than two. In rabbits, for example, there is a **C** gene which causes colored coat, while the homozygous recessive (**cc**) causes albino coat. Two other genes located at the same locus and inherited allelomorphically, are $\mathbf{c^h}$ and $\mathbf{c^{ch}}$. The gene $\mathbf{c^h}$, when homozygous, causes the "Himalayan" pattern, in which the rabbit's body is white, but the tips of the ears, nose, tail and legs are colored. The $\mathbf{c^{ch}}$ gene, when homozygous, produces the "Chinchilla" pattern, a light gray color all over the body. These genes may be arranged in a series, **C**, $\mathbf{c^{ch}}$, $\mathbf{c^h}$, **c**, in which each gene is dominant to the genes following it, and recessive to those preceding it. From this it follows that $\mathbf{c^hc}$ produces a "Himalayan" phenotype. In other series of multiple alleles, the genes may be incompletely dominant, so that a heterozygote (called a **compound**) has a phenotype intermediate between those of its parents.

An important characteristic in man, inherited by multiple alleles, is the type of blood: O, A, B or AB (see also p. 139). There are three alleles in this series: gene **A**, which causes the formation of agglutinogen **A**; gene $\mathbf{A^B}$, which causes the formation of agglutinogen **B**; and gene **a**, which produces no agglutinogen. Gene **a** is recessive to the other two, but neither gene **A** nor $\mathbf{A^B}$ is dominant to the other. A compound of the two causes the formation of both agglutinogens, so that the individual is of blood group AB. Because the blood types are determined genetically and do not change in a person's lifetime, blood tests can be helpful in settling cases of disputed parentage. It must be emphasized that a blood test can never prove that a certain man *is* the father of a certain child, but only whether he *could be* its father (see Table 11). Two other independent sets of blood types are the **M-N** factors and the series of **Rh** alleles.

The frequency of the various blood types differs in different races. Among native white Americans the frequencies are as follows: 41 per cent, O; 45 per cent, A; 10 per cent, B; and 4 per cent, AB. Among American Indians, the frequencies of A and B are almost reversed. Some interesting work combining anthropology and genetics has been done in tracing the relationships of different races as determined by the relative frequency of these blood types.

5. Lethal Genes. Certain genes known as lethal genes cause such a tremendous deviation from the normal development of an organism that

it is unable to survive. The existenee of these genes is deteeted by upsets in genetic ratios. For example, in a eertain strain of miee, although yellow coat color was exhibited, experimenters found it impossible to establish a true breeding strain for yellow coat. Instead, when two yellow mice were bred, offspring in the ratio of two yellow: one black oecurred! A yellow mouse bred to a black mouse gave 50 per eent yellow

Table 11. Exclusion of Paternity Based on Blood Type Tests

Child	Mother	Father Must Be of Type	Father Cannot Be of Type
O	O	O, A, B	AB
O	A	O, A, B	AB
O	B	O, A, B	AB
A	O	A, AB	O, B
A	A	A, B, AB, O	——
B	B	A, B, AB, O	——
A	B	A, AB	O, B
B	A	B, AB	O, A
B	O	B, AB	O, A
AB	A	B, AB	O, A
AB	B	A, AB	O, B
AB	AB	A, B, AB	O

and 50 per cent black offspring. In this way, yellow was proved to be dominant to black. The investigators noticed that the litters of yellow $\times$ yellow matings were only three quarters as large as other mice litters. Evidently, one quarter of the embryos (those homozygous for yellow) did not develop. Using A^Y for the yellow gene and **a** for its recessive allele (black), the yellow $\times$ yellow mating results in the following (Fig 210):

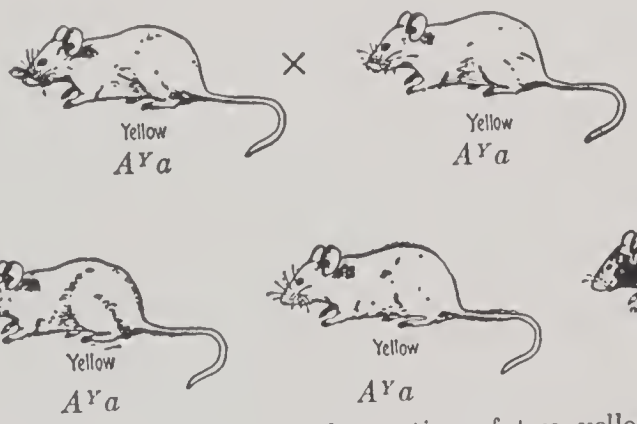


Fig. 210. A cross involving lethal genes: the mating of two yellow mice produces offspring in the ratio of two yellow to one black. (Sinnott and Dunn: Principles of Genetics, McGraw-Hill Book Co., Inc.)

Later research showed that the homozygous, yellow mice began development, then stopped, died and were resorbed. If the uterus of the mother is opened early in pregnancy, the abnormal embryos are visible.

An exactly similar situation oceurs in chiekens. "Creeper" fowl have short legs and shorter wings than normal. When two "creepers" are bred, the offspring are two "ereepers": one normal. One quarter of the eggs—those homozygous for "creeper"—have marked abnormalities of the vertebras and spinal cord, and die without hatching.

These lethal genes, yellow and "creeper," produce a phenotypic effect when heterozygous and so are considered dominant. Many—perhaps most—lethal genes have no effect when heterozygous, but cause death when homozygous, and therefore are called recessive lethal genes. These can be detected only by special genetic techniques. Analyses of wild populations of fruit flies (*Drosophila*), made by these special techniques, have revealed many recessive lethals.

Several genes are suspected of being lethal in human embryos, one of which is a dominant gene for brachyphalangy (short fingers). Mohr and Wriedt reported a case in which two people with this defect married and produced a child with no fingers or toes, who died immediately.

III. THE GENETIC DETERMINATION OF SEX

The sex of an organism is another trait which is determined genetically. There is one exception to the general rule that all homologous pairs of chromosomes are identical in size and shape: the **sex chromosomes.** In females there are two identical sex chromosomes, called **X** chromosomes, but in males there is only one **X** chromosome, and a smaller one called **Y.** The latter contains few or no genes and is, in most species, of a different size and shape from the **X** chromosome, yet in meiosis in the male, **X** and **Y** undergo synapsis and then separate. Men, therefore, have twenty-three pairs of ordinary chromosomes, plus an **X** and a **Y** chromosome; women have twenty-three pairs of ordinary chromosomes, plus two **X** chromosomes. But it is not the **Y** chromosome which determines maleness. An animal may have no **Y** chromosome at all (only an **X**) and be male, although he will probably be sterile. Whether a person is male or female is determined by whether there is one or two **X** chromosomes.

The work of C. B. Bridges shows that in fruit flies, sex is determined by the ratio of the number of **X** chromosomes to the number of haploid sets of other chromosomes. Thus, in males, there is one **X** to two haploid sets of other chromosomes, a ratio of 1:2 or 0.5. In females there are two X chromosomes to two sets of other chromosomes, a ratio of 1.0. Now, by certain genetic techniques possible in fruit flies, Bridges set up abnormal flies with a ratio of 0.33 which had all their male characteristics exaggerated, and which he named "supermales." He also set up abnormal individuals with the ratio of 1.5 sex chromosomes to sets of ordinary chromosomes, which had all the female characteristics exaggerated and which he named "superfemales." The ratio 0.67 produced animals called **intersexes,** with characters intermediate between males and females. These abnormal flies, "supermales," "superfemales," and intersexes, are all sterile.

All eggs produced by females have one **X** chromosome. Half of the sperm produced by males contain an **X** chromosome and half contain a **Y.** The fertilization of an **X**-bearing egg by an **X**-bearing sperm results in an **XX**—female—zygote. The fertilization of an **X**-bearing egg by a **Y**-bearing sperm results in an **XY**—male—zygote. Since there are equal numbers of **X**-and **Y**-bearing sperm, about equal numbers of each sex are born. Actually, about 107 boys are born to every 100 girls, and the ratio of males to females at conception is even higher. This is explained by the fact that the **Y** chromosome is smaller than the **X** chromosome,

so that sperm containing a **Y** chromosome are lighter and can swim a little faster than **X**-bearing sperm; consequently, they are able to win the race to the egg slightly more than half the time. The ratio of males to females at conception is about 114:100. But during intra-uterine development, more boys than girls die, so that the ratio at birth is 107 to 100. After birth this differential death rate continues, and by the age of ten or twelve there are equal numbers of males and females, after which there is a majority of females.

This mechanism is believed to operate in all species with separate sexes. In some animals—birds and butterflies (Lepidoptera)—the mechanism is reversed: males are **XX** and females **XY**. Sex chromosomes have been detected in some plants—notably, strawberries—and probably exist in other plants with separate sexes. Remember that the members of many species have the organs of both sexes. In such organisms (called hermaphroditic if animals, and monoecious if plants) sex chromosomes have not been found.

6. Sex-Linked Characteristics. The **X** chromosome contains many genes; the **Y** chromosome contains only a few. The traits controlled by genes lying in the **X** chromosome are called sex-linked, because their inheritance is linked with that of sex. Male offspring receive their single **X** chromosome (and all the genes for sex-linked characters) from their mothers. A female receives one **X** from her mother and one from her father. A male zygote, having but one **X** chromosome, has only one of each gene located in the **X** chromosome. To avoid confusion, its genotype is written with the **Y**. Thus if **A** is a sex-linked gene, the genotype for a female is **AA** (she has two **XX** chromosomes and each contains an **A** gene). The genotype for a male is **AY** (he has one **X** chromosome containing the **A** and one **Y** chromosome which does not contain an **A** gene).

In fruit flies, one of the classic subjects of genetic research because a new generation appears every ten days, the normal eye color is dark red, but white-eyed forms do occur. The genes for red or white eye color are located in the **X** chromosome and hence are sex-linked. Red eye color (**R**) is dominant to white (**r**). In sex-linked inheritance the traits of the offspring depend upon the sex of the parent which had a particular trait. Crossing a homozygous, red-eyed female with a white-eyed male (**RR** $\times$ **rY**) produces all red-eyed offspring (**Rr** females and **RY** males). Crossing a white-eyed female with a red-eyed male (**rr** $\times$ **RY**) produces offspring in which all the females are red-eyed (**Rr**) and all the males are white-eyed (**rY**). Make the proper checkerboard to prove this.

Many sex-linked traits are known. In man, hemophilia (bleeder's disease) and color blindness are sex-linked. Because of this, a color-blind man with a color-blind father and a normal-visioned mother, inherits his color blindness from his mother (who would have to be heterozygous) and not from his father!

7. Sex-Influenced Characters. Not all the characters which differ in the two sexes are sex-linked; some, known as sex-influenced traits, are inherited by genes which, though not located in the sex chromosomes, are altered or influenced by the sex of the animal. Thus the same genotype may produce a different phenotype in a male from that produced in a female. In sheep, a single pair of genes determines the presence or

absence of horns. The gene **H**, for the presence of horns, is dominant in males, but recessive in females, and its allelomorphic gene, **h**, for hornlessness is recessive in males, but dominant in females. Therefore, the genotype **HH** produces a horned animal, regardless of sex; **Hh** produces the horned phenotype if the animal is male, the hornless one if the animal is female; and **hh** produces a hornless animal whether it is a ram or a ewe.

In Ayrshire cattle the inheritance of mahogany-and-white spotted coat and its allelomorph, red-and-white spotted coat, is sex-influenced. The gene, **M**, for mahogany-and-white is dominant to the gene **m** for red-and-white, in males, but recessive to it in females. Thus the genotype **MM** produces a mahogany-and-white male or female, and **mm** produces a red-and-white male or female. But **Mm** produces a mahogany-spotted coat if the animal is male and a red-spotted coat if the animal is female.

In man the gene for pattern baldness is sex-influenced, its expression being altered by the amount of male sex hormone present. It is dominant in males and recessive in females. There are many more bald men than women because only one gene for baldness will cause a man to lose his hair, while two genes are needed to produce a bald woman. Supposing **B** to be the gene for baldness, and **b** to be the gene for nonbaldness, the genotype **BB** produces baldness in men and women; **Bb** produces baldness in men but not in women; and **bb** causes baldness in neither. Not all baldness is hereditary, of course; some types are caused by disease or other factors.

In working a problem involving a sex-influenced gene, the result must be stated separately for the two sexes. Therefore, the offspring of a heterozygous bald man (**Bb**) and a heterozygous nonbald woman (**Bb**) will be in the ratio of three bald to one nonbald, if male, but three nonbald to one bald, if female.

IV. LINKAGE AND CROSSING OVER

In discussing the simultaneous inheritance of two pairs of genes, we stressed the pointed that to get a 9:3:3:1 ratio, the pairs of genes must lie in different (nonhomologous) chromosomes. Since there are only twenty-four pairs of chromosomes and many hundreds of different inherited traits, it is obvious that there must be many genes in each chromosome. All the genes in each chromosome tend to be inherited as a group and are said to be *linked*. This is due to the fact that in meiosis the homologous pairs of chromosomes separate *as units* and go to opposite poles. Therefore, all the genes lying in one chromosome go to one pole to become incorporated in one gamete, and all the genes contained in the other member of the homologous pair go to the other pole and become incorporated in another gamete.

Linkage between the genes in a given chromosome is usually not complete, however. During the process of synapsis the homologous chromosomes frequently exchange whole segments of chromosome material and the genes located in them. The exact mechanism of this exchange is still unknown, but it occurs at random along the length of the chromosomes. Therefore, the greater the distance between the loci of any two

given genes in a chromosome, the greater is the chance that an exchange of segments will occur between them. The exchange of segments between homologous chromosomes, called **crossing over,** makes possible new combinations of linked genes. In tomatoes, the genes **T** (tall) and **t** (dwarf), and **S** (spherical fruits) and **s** (pear-shaped fruits) are both

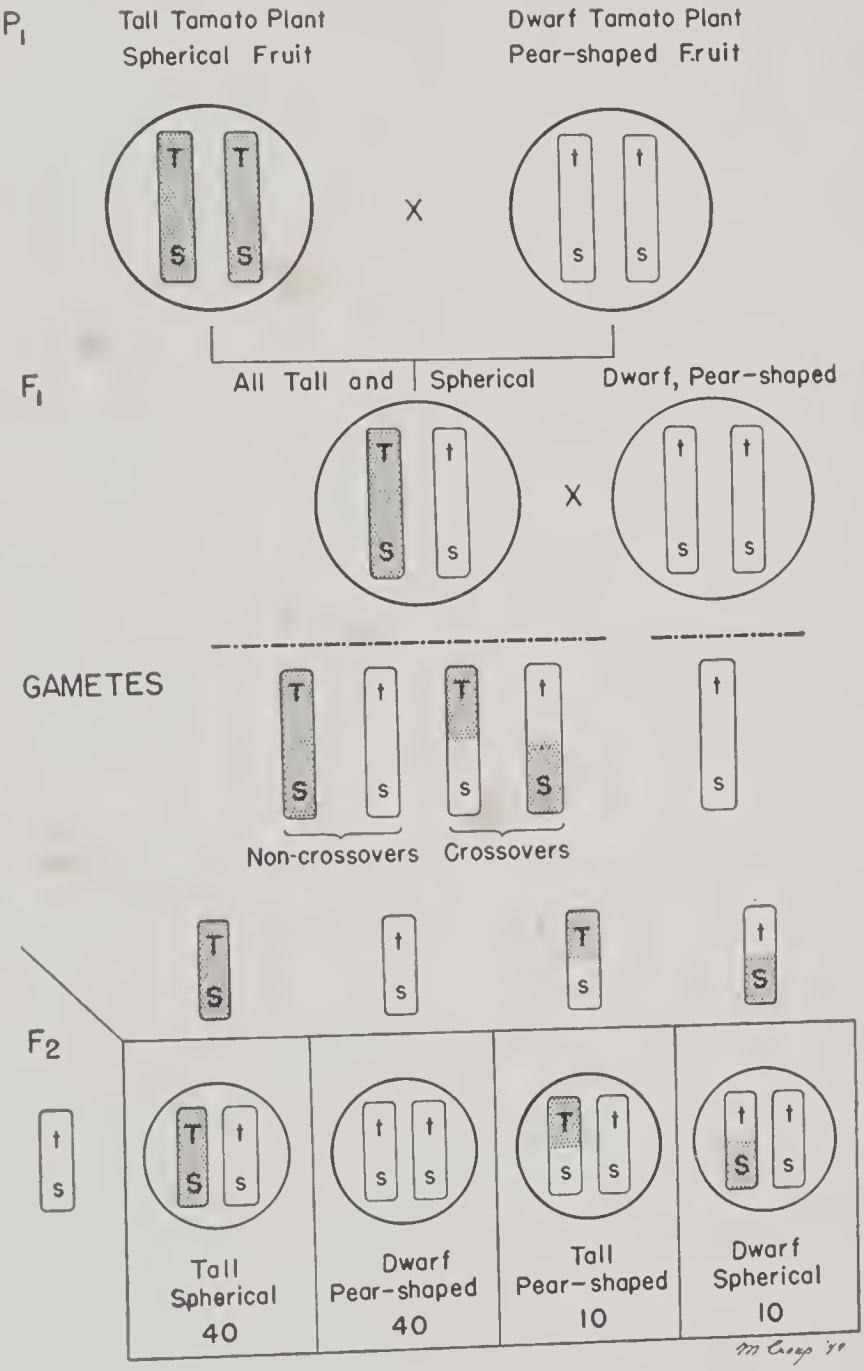


Fig. 211. Diagram of a cross involving linkage and crossing over. The genes for tall vs. dwarf, and spherical vs. pear-shaped fruit in tomatoes, are linked; they are located in the same chromosome.

located in the same chromosome and are linked, **T** lying near one end, and **S** close to the other end of the chromosome. If a homozygous **TTSS** plant is crossed with a homozygous **ttss** plant (Fig. 211), the offspring are all tall plants with spherical fruit, but genetically heterozygous, **TtSs**. So far, there would appear to be no difference from the case in which the genes lie in different chromosomes. However, when one of the F_1 heterozygotes is crossed with a homozygous recessive **ttss**, the differ-

ence is apparent. If the genes were not linked, but were in different chromosomes, the offspring would be in the ratio of one tall, spherical: one dwarf, spherical: one tall, pear-shaped: one dwarf, pear-shaped. If the genes were completely linked and no crossing over occurred, only tall, spherical and dwarf, pear-shaped plants would appear, and these would be in equal numbers. Even with crossing over occurring, most of the offspring are either tall and spherical, or dwarf and pear-shaped (noncrossovers), and only those few in which an exchange took place in the chromosome between **T** and **S** are tall and pear-shaped, or dwarf and spherical (crossovers). This crossing over occurs 20 per cent of the time, and offspring are in the ratio of forty tall, spherical: forty dwarf, pear-shaped: ten tall, pear-shaped: ten dwarf, spherical.

The facts of crossing over provide proof that the genes lie in a linear order in the chromosomes. If three genes **A, B** and **C** lie in the same chromosome, and tests show that crossing over between **A** and **B** occurs 5 per cent of the time, and crossing over between **B** and **C** occurs 3 per cent of the time, then, when the percentage of crossing over between **A** and **C** is tested, it will be found to be either 8 per cent or 2 per cent. If it is 8 per cent, **C** lies to the right of **B** and the order is as follows: $\underbrace{\underbrace{A \quad B}_{5\%} \quad C}_{8\%}$. If it is 2 per cent, then **C** lies between **A** and **B** and the order is like this: $\underbrace{A \quad \underbrace{C \quad B}_{3\%}}_{5\%}$. In all tests of crossing over the percentage of crossing over between the first and third gene is either the sum of or the difference between the percentages of crossing of the first and second, and the second and third. These facts are only explained by assuming that the genes lie in a linear order in the chromosome.

All the genes in a particular chromosome constitute a **linkage group.** These groups, which, of course, are determined genetically, always equal in number and never exceed the haploid number of chromosomes. This is additional confirmation of the fact that the genes are located in the chromosomes. Linkage groups remain constant and are only changed by a **translocation** in which a piece of one chromosome breaks off and becomes attached to another, nonhomologous chromosome (see p. 476). The linkage between two particular genes, such as the linkage between tall and spherical, is called a **specific linkage.** These may be changed by crossing over so that tall becomes linked to pear-shaped. That is, through an exchange of segments between homologous chromosomes, the gene for tall plants and the gene for pear-shaped fruit come to lie in the same chromosome. It is beyond the scope of this text to discuss further the complexities which linkage and crossing over add to inheritance.

V. PENETRANCE AND EXPRESSIVITY

In all the genes discussed so far, each recessive gene produces its trait when it is homozygous, and each dominant gene produces its ef-

fect when it is homozygous or heterozygous. This is not true for all genes —geneticists have found some which do not always produce their phenotypes when they should. Genes such as the ones we have discussed so far, which always produce the expected phenotype, are said to have complete or 100 per cent **penetrance.** If only 70 per cent of the individuals of a stock homozygous for a certain recessive gene show the character phenotypically, however, then the gene is said to show 70 per cent penetrance. The percentage of penetrance of genes showing incomplete penetrance may be altered by changing the conditions of temperature, moisture, nutrition, and so forth, under which the organism develops.

Some stocks which are homozygous for a certain gene may exhibit wide variations in the appearance of the character. Fruit flies of a stock homozygous for a gene producing shortening and scalloping of the wings may exhibit wide variations in the degree of shortening and scalloping. Such differences are known as variations in the **expressivity,** or **expression,** of the gene. The expressivity of a gene may be altered also by changing environmental conditions during the organism's development.

VI. INBREEDING AND OUTBREEDING

It is commonly believed that inbreeding—the mating of two closely related organisms such as brother and sister—is harmful and leads to the production of idiots and monstrosities. Even the marriage of first cousins is forbidden by law in some states. There is nothing harmful, however, in the act of inbreeding itself. Commercial breeders use inbreeding constantly to improve their strains of cattle, wheat, hens or cantaloupes. It is not necessarily a bad practice in human beings; it simply provides a greater chance for recessive genes to become homozygous and express themselves phenotypically. All organisms are heterozygous for many characters, some of the recessive genes so hidden being for desirable characters, while others are for undesirable ones. If a stock is good, inbreeding will improve it; if a stock has many undesirable recessive traits, inbreeding will cause some of them to appear phenotypically.

The opposite of inbreeding is outbreeding, in which totally unrelated strains are bred. Frequently, as a result of this, the offspring are much better than either parent, a phenomenon known as **hybrid vigor.** A mule, the hybrid resulting from the mating of a horse and a donkey, is a strong and sturdy beast, more vigorous than either parent. A large part of the corn grown in the United States is a special hybrid developed by the United States Department of Agriculture from a mating of four different strains (Fig. 212). Each year, the seed to grow this uniformly fine hybrid corn must be obtained by mating the original strains, for the hybrid, being heterozygous, would give rise to a great variety of forms, probably none of which would be as good as the original hybrid.

The explanation of hybrid vigor is as follows: in the corn, each of the parental strains is homozygous for certain undesirable recessive genes, but the two strains are homozygous for *different* genes, and each has dominant ones to mask the undesirable recessive genes of the other. Let

us consider just four pairs of characters, **A, B, C,** and **D,** the capital letters standing for some dominant desirable trait, the lower-case letters for their recessive, undesirable alleles. One strain, then, might have the

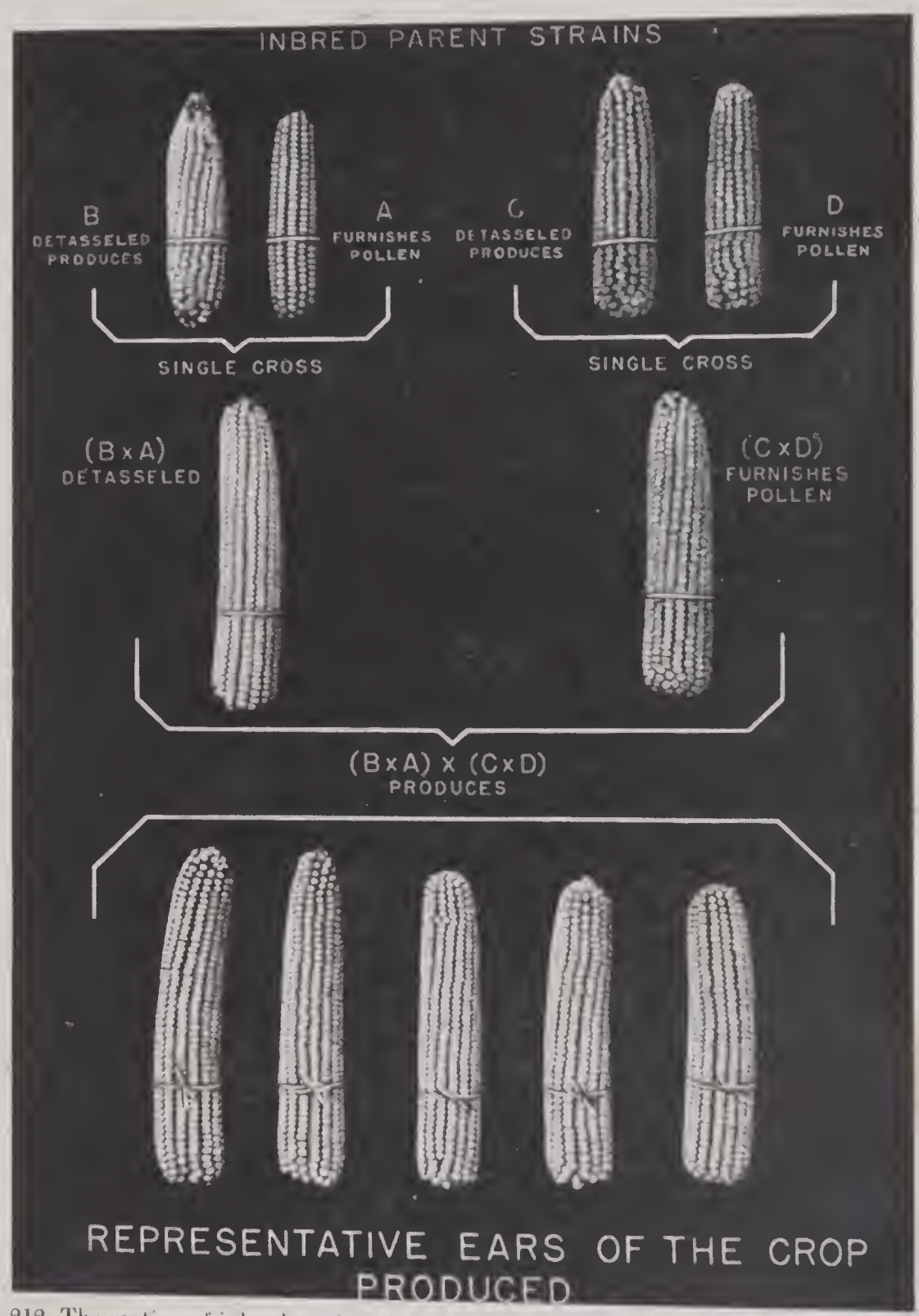


Fig. 212. The mating of inbred strains of corn to produce the commercial variety with strong hybrid vigor. (Courtesy of the United States Department of Agriculture.)

genotype **AAbbCCdd,** and the other, **aaBBccDD.** The hybrid offspring would be **AaBbCcDd,** combining all the desirable and none of the undesirable traits. The actual situation in corn is, of course, much more complicated than this.

VII. BIOCHEMICAL GENETICS

For the last ten or fifteen years, geneticists have not been content with the statement that a particular gene produces blue or brown eyes in man, or round or wrinkled peas, but have endeavored to discover the actual chemical and physical mechanisms involved. Today, there is enough information about this field—which involves a combination of genetics, embryology and biochemistry—to form the basis of a new science, that of **biochemical genetics.** This science concerns two principal, interrelated problems: (a) the chemical and physical nature of genes, and (b) the mechanism whereby these genes control the development and maintenance of the organism.

There is now good experimental evidence that genes belong to the class of chemical compounds known as nucleoproteins, which are composed of proteins and nucleic acids. The latter are found in all biological substances capable of self-reproduction—viruses, chloroplasts and mitochondria, as well as genes. But whether it is the protein or the nucleic acid part of the gene, or both, which gives it its unique quality (enables it to produce a blue eye, for instance) is not known.

The work of Drs. G. W. Beadle and E. L. Tatum and their collaborators has done much to indicate how genes function in the control of development. Their hypothesis is that each gene manufactures a particular enzyme which, in turn, regulates a particular step in the synthesis of the chemical compound appearing as the end result. Consider how this works in a specific case. In guinea pigs **B** is a gene for black coat, and **b** a gene for white coat. Now, the blackness of the coat is caused by a pigment known as melanin, produced by the oxidation of a chemical, dihydroxyphenylalanine (called "dopa" for short) by a specific enzyme, dopa oxidase. The gene **b** differs from the gene **B** in such a way that the enzyme dopa oxidase is not produced, so that melanin is not formed, and consequently the fur is white.

Beadle and Tatum have been able to show that the synthesis of all kinds of chemicals by the baker's mold, *Neurospora,* depends upon the action of genes. Usually, the synthesis of a chemical compound requires several different steps, each controlled by a different enzyme, made by a different gene. By exposing baker's mold to X-rays or ultraviolet rays, these investigators have produced hundreds of mutations in which the synthesis of some chemical compound required for growth was interfered with. In each case, the mutant strain was found to differ from the normal by only a single gene, and the mutant could be made to grow normally if supplied with a single chemical—a vitamin, an amino acid, or something else—indicating that each gene produces a single enzyme regulating one step in the biological synthesis of that compound.

In man, similar one-to-one relationships between gene, enzyme and biochemical reaction are known. The most famous of these results in the abnormal condition known as **alcaptonuria,** in which a person's urine turns black upon standing for a while. This peculiarity is inherited through a single pair of recessive genes. The substance in the urine which turns black is homogentisic acid, and normal people have an enzyme which oxidizes it so that it is excreted as carbon dioxide and water. People with alcaptonuria lack the gene to make this enzyme,

and in its absence, homogentisic acid accumulates in the blood and spills over into the urine, causing it to turn black. No harmful effects appear to be associated with this abnormality.

One of the major unsolved problems of biochemical genetics is how all the various tissues of the body become established in the right places. From the discussion of the regularity of the mitotic process, it is clear that every cell of the body has exactly the same number and kind of genes as every other one, yet the end results of their activities vary remarkably. The differences must somehow be due to the different metabolic effects of the same genes working in various cytoplasmic environments.

One of the clearest demonstrations that the same genes working in dissimilar environments do have different effects was provided by experiments with three races of frogs found naturally in Florida, Pennsylvania and Vermont. Each of these types normally develops at a certain speed which is adapted to the normal length of the spring and summer seasons, Southern frogs developing slowly, and Northern frogs more rapidly. Northern frogs raised in Southern conditions were overaccelerated in development, while Southern frogs raised in Northern conditions were overretarded. By fertilizing an egg with sperm from a different race, and then removing the egg nucleus before the sperm nucleus united with it, it was possible to set up "Northern" genes operating in "Southern" cytoplasm. This resulted in poorly regulated development, and the animal's head, growing more rapidly than the posterior region, was disproportionately large. When "Southern" genes were introduced into "Northern" cytoplasm, again there was poorly regulated development, but with the head, rather than the posterior region, retarded, causing it to be disproportionately small. Genes from the Pennsylvania race acted as "Northern" with Florida cytoplasm, and as "Southern" with Vermont cytoplasm. Thus, exactly the same set of genes produced opposite morphological effects when operating in different environments.

QUESTIONS

1. Show by diagrams how genes located in different pairs of chromosomes segregate independently in meiosis.

2. In peas, yellow color (Y) is dominant to green (y) and smooth peas (S) are dominant to wrinkled ones (s). Give the genotypic and phenotypic ratios of the offspring of the following crosses:

   (*a*) YYss × yySS
   (*b*) YySs × YySs
   (*c*) YySs × yyss
   (*d*) Yyss × yySs

3. In rabbits, spotted coat (S) is dominant to solid colors (s) and black (B) is dominant to brown (b). A brown spotted rabbit is mated to a solid black one and all the offspring are black spotted. What are the genotypes of the parents? What would be the appearance of the F_2 if two of these F_1 black spotted rabbits were mated?

4. The long hair of Persian cats is recessive to the short hair of Siamese cats, but the black coat color of Persians is dominant to the black-and-tan coat of Siamese. If a pure black, long-haired Persian is mated to a pure black-and-tan, short-haired Siamese, what will be the appearance of the F_1? If two of these F_1 cats are mated, what is the chance of obtaining in the F_2 a long-haired, black-and-tan cat?

5. In peas, tall plants (T) are dominant to dwarf (t). What would be the phenotypes of the offspring of the following matings?

   (*a*) TtYySs × ttyyss
   (*b*) TtyySs × ttYySs

6. Define the following: complementary genes, supplementary genes, multiple factors, multiple alleles, sex-linked character, sex-influenced character, penetrance.

7. A walnut-combed rooster is mated to three hens. Hen A, which is walnut-combed, has offspring in the ratio of 3 walnut: 1 rose. Hen B, which is pea-combed, has offspring in the ratio of 3 walnut: 3 pea: 1 rose: 1 single. Hen C, which is walnut-combed, has only walnut-combed offspring. What are the genotypes of the rooster and the three hens?

8. What conditions result in the following phenotypic ratios: 3:1, 1:2: 1, 9: 3: 3: 1, 9: 7, 1: 4: 6: 4: 1, 2: 1, 47: 47: 3: 3?

9. The weight of the fruit in one variety of squash is determined by three pairs of genes, **AABBCC** producing 6-pound squashes, **aabbcc** producing 3-pound squashes. Each dominant gene adds one-half pound to the weight. When a 6-pound squash is mated to a 3-pound squash, all the offspring weigh 4½ pounds. What would be the weights of the F_2 fruits if two of these F_1 plants were mated?

10. Mrs. Smith and Mrs. Roe had babies at the same hospital at the same time. Mrs. Smith took home a girl and named her Nancy. Mrs. Roe received a boy and named him Richard. Mrs. Roe was sure, however, that she had had a girl, and brought suit against the hospital. Blood tests showed that Mr. Roe was type O, Mrs. Roe type AB, Mr. and Mrs. Smith were both type B, Nancy was type A, and Richard, type O. Had an exchange occurred?

11. A gene **l**, known in fruit flies, is sex-linked, recessive, and lethal. If a normal male is mated to a female heterozygous for this gene, what will be the sex ratio of their offspring?

12. Explain the mechanism of the genetic determination of sex.

13. One pair of genes for coat color in cats is sex-linked. **B** produces yellow coat, **b** produces black coat, and the heterozygote, **Bb**, produces tortoise-shell. What kind of offspring result from the mating of a black male and a tortoise-shell female?

14. A bald, normal-visioned man whose father was not bald, marries a nonbald, normal-visioned woman whose father was color-blind and whose mother was bald. What types of offspring may they have?

15. What is meant by linkage? By crossing over?

16. What are the advantages and disadvantages of inbreeding?

17. What is meant by hybrid vigor? What is the genetic explanation of this phenomenon?

SUPPLEMENTARY READINGS

Beadle, G. W.: in *Science in Progress*. New Haven, Yale University Press, 1949, Vol. 6.
A clear, readable, popular discussion of some aspects of biochemical genetics.

Sinnott, E. W., and Dunn, L. C.: *Principles of Genetics*. 3rd ed. New York, McGraw-Hill Book Company, Inc., 1939.
An understandable, detailed presentation of modern genetics.

Sturtevant, H. H., and Beadle, G. W.: *An Introduction to Genetics*. Philadelphia, W. B. Saunders Company, 1939.
A detailed, more advanced discussion of genetics and cytogenetics.

CHAPTER 25

INHERITANCE IN MAN

MOST LAYMEN, and, unfortunately, some biologists and physicians have the idea that little or nothing is known about human inheritance except that some things "seem to run in families." This is far from true. A great deal of information about heredity in man has been accumulated, and research in this field is still going forward rapidly as new techniques involving statistical methods are devised.

Inheritance in man depends upon the same principles as inheritance in plants and other animals. Human traits may be controlled by multiple factors, multiple alleles, sex-linked genes and all other types of inheritance mentioned in the last chapter. It is more difficult to study inheritance in man than in animals and plants because some of the techniques such as test crosses and progeny tests are obviously impossible.

When studies of human heredity were first initiated, geneticists depended solely upon the accumulation of family histories, or pedigrees,

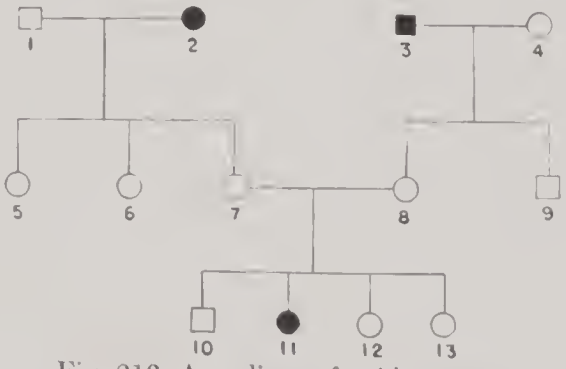


Fig. 213. A pedigree for blue eyes.

for their knowledge of the specific method involved in the inheritance of trait. But since 1925, a new tool, statistics, has been of increasing value in interpreting the raw material, by indicating the probability that a certain type of inheritance is involved.

The age at which a particular gene expresses itself phenotypically varies widely with different characteristics. Most of them develop long before birth, although some, including hair and eye color, may not appear until later. Others, such as amaurotic idiocy, become evident in childhood, and a few, such as glaucoma, develop only after the individual has reached maturity.

I. PEDIGREES

In pedigree diagrams, males are indicated by squares, and females, by circles. Individuals showing the particular trait in question are colored, those not showing the character are left blank. Relationship is indicated by connecting lines, and all the individuals of the same genera-

tion are placed in the same row. The pedigree in Fig. 213 reveals that No. 11 is a blue-eyed girl, while her two sisters (12 and 13) and her brother (10), as well as her mother (8) and father (7), are all brown-eyed. Her two aunts (5 and 6), an uncle (9), her paternal grandfather (1) and maternal grandmother (4) are brown-eyed, but her paternal grandmother (2) and maternal grandfather (3) are blue-eyed. Her parents are, of course, heterozygous for blue eyes. Pedigrees for recessive traits are characterized by this "skipping of a generation."

II. THE INHERITANCE OF PHYSICAL TRAITS

The development of every organ of the body is regulated by genes, some of which are now known in spite of the difficulties involved in studying human inheritance. Table 12 lists some of the human traits known to be hereditary, arranged according to the system involved. Some of the conditions are caused by dominant genes in one pedigree, and by recessive genes in another.

Table 12. Some Traits in Man Known to Be Inherited

Dominant	Recessive
Hair, Skin, Nails, Teeth	
Dark hair	Blond hair
Nonred hair	Red hair
Curly hair	Straight hair
Abundant body hair	Little body hair
Early baldness (dominant in male)	Normal
White forelock	Self-color
Piebald (skin and hair spotted with white)	Self-color
Pigmented skin, hair, eyes	Albinism
Black skin (2 pairs of genes, dominance incomplete)	White skin
Ichthyosis (scaly skin)	Normal
Epidermis bullosa (sensitiveness to slight abrasions)	Normal
Absence of enamel of teeth	Normal
Normal	Absence of sweat glands
Eyes	
Brown	Blue or gray
Hazel or green	Blue or gray
"Mongolian fold" (extra fold of skin in Chinese and Japanese)	No fold
Congenital cataract	Normal
Nearsightedness	Normal vision
Farsightedness	Normal vision
Astigmatism	Normal vision
Glaucoma	Normal
Aniridia (absence of iris)	Normal
Congenital displacement of lens	Normal
Normal	Optic atrophy (sex linked)
Normal	*Microphthalmus*
Features	
Free ear lobes	Attached ear lobes
Broad lips	Thin lips
Large eyes	Small eyes
Long eyelashes	Short eyelashes
Broad nostrils	Narrow nostrils
High, narrow bridge of nose	Low, broad bridge
"Roman" nose	Straight nose

Table 12. Some Traits in Man Known to Be Inherited (continued)

Dominant	Recessive
Skeleton and muscles	
Short stature (many genes)	Tall stature
Achondroplasia (dwarfism)	Normal
Ateliosis (midget)	Normal
Polydactyly (more than 5 digits on hands or feet)	Normal
Syndactyly (webbing of 2 or more fingers or toes)	Normal
Brachydactyly (short digits)	Normal
Cartilaginous growths on bones	Normal
Normal	Club foot (not always inherited)
Normal	Progressive muscular atrophy (sex-linked)
Circulatory and Respiratory Systems	
Hereditary edema (Milroy's disease)	Normal
Blood groups A, B, and AB	Blood group O
Hypertension (high blood pressure)	Normal
Resistance to tuberculosis	Susceptibility to tuberculosis
Normal	Hemophilia (sex-linked)
Anemia (certain types)	Normal
Excretory System	
Polycystic kidney	Normal
Endocrine System	
Diabetes mellitus (low penetrance)	Normal
Digestive System	
Enlarged colon (Hirschsprung's disease)	Normal
Nervous System	
Tasters (of phenylthiocarbamide)	Nontasters
Normal	Congenital deafness
Normal	Spinal ataxia
Huntington's chorea	Normal
Normal	Amaurotic idiocy
Migraine (sick headache)	Normal
Normal	Dementia praecox (several pairs of genes involved)
Normal	Phenylketonuria (type of imbecility)
Paralysis agitans	Normal
Cancers	
Normal	Xeroderma pigmentosum
Recklinghausen's disease	Normal
Normal	Retinal glioma

The color of hair in man is regulated by several genes. Blond hair is recessive to dark hair, but the production of different shades of dark or light hair is due to the interactions of several pairs of modifying factors. Red hair is caused by a single gene which is recessive to the gene for nonred hair. True red hair appears only in a person also homozygous for blonde hair genes. In a person homozygous for red hair, who also has genes for dark hair (these need not be homozygous), the red pigment is masked by the dark pigment, and dark hair with a reddish tint results. Curly hair is not completely dominant to straight hair—the heterozygous condition produces wavy hair.

Eye color is regulated by the amount and location of pigment in the iris. The pink eyes of albinos are really colorless, the effect of pinkness being due to a reflection from blood vessels in the iris and back of the eye. Nor do blue eyes contain blue pigment; in this case, it is dark pigment in the back of the iris from which light is reflected to produce the impression of color. If such an iris has a small amount of yellow pigment in the front of the iris, a green eye results. A scattering of dark pigment in the front of the iris produces a gray eye. A brown or black eye is due to heavy concentration of pigment in the front of the iris. The **"Mongolian fold"** of the eye is a piece of skin extending from the upper lid down over the inner corner of the eye, which gives the Chinese and Japanese their slant-eyed appearance. This fold is not limited to the Mongolian race, however.

The **"Mongolian spot,"** an irregular, bluish mark which appears in the lumbar region of newborn babies, may be as small as a pea or as large as an apple, but it usually fades out in childhood. It occurs almost universally in Mongolians, frequently in members of the black and brown races, and rarely in whites. It does not necessarily indicate Mongolian ancestry. *Epidermis bullosa* is an abnormality in which blisters of various sizes appear on the skin, especially of the hands and feet, in response to slight friction. People with this condition have difficulty wearing shoes, and must wear loose-fitting clothing. Another inherited abnormality is the complete absence of sweat glands, which is usually accompanied by scanty hair and a deficient number of teeth. A person with this abnormality suffers terribly from heat, and in hot weather must frequently immerse himself in water.

Some hereditary factors produce such a striking abnormality that the person is classed as a freak. The condition known as **hypertrichosis** is caused by a dominant gene which causes the embryonic hair—normally shed before birth—to remain and grow excessively throughout life, resulting in the "dog-faced man" of the circus sideshow. The "porcupine man" of the circus suffers from **ichthyosis,** in which a dominant gene produces a dry skin covered with flakes or scales that are constantly being shed.

Most of the skeletal and muscular conditions mentioned in the table are self-explanatory. The short fingers and toes of the brachydactylous condition are usually due to the absence of the middle phalanx of each digit. Progressive atrophy of the muscles is a recessive, sex-linked character in which the muscles, especially those of the calves of the legs, atrophy or wither. The condition appears before a child is ten years old and becomes progressively worse; death usually ensues within ten years.

We have previously discussed the inheritance of hemophilia and the blood groups. **Milroy's disease** is a hereditary condition in which the blood vessels of the extremities are weak and an excessive amount of plasma passes from the vessels into the tissues, causing the swollen, "watery" condition known as **edema.**

Some, but not all, cases of hypertension, or high blood pressure, have a genetic cause. Children of parents with high blood pressure should have regular medical examinations, and at the first sign of hypertension should refrain from strenuous sports and overexcitement, and lose weight if necessary.

People differ in their ability to taste certain things. The first accurate study of this was made by using a chemical, phenylthiocarbamide, which some people report to be completely tasteless and others find to have a bitter taste. The inheritance of "tasting" versus "nontasting" is controlled by a single pair of genes, "tasting" being dominant to "nontasting."

III. INHERITANCE OF MENTAL QUALITIES

At one time a bitter argument raged over whether heredity or environment was the more important in determining human characteristics. We now know that mental traits develop under the influence of genes, just as physical traits do, but that the final result of both depends upon the interaction of genes with the environment. For some characteristics, genes play the dominant role; for others, environment seems to be more important.

Mental traits are particularly difficult to study genetically. Such qualities as attitude, temperament and intelligence are difficult to define and measure, and it is sometimes impossible to distinguish between different types of mental disorders. But other types of mental disorders are distinctive, and their inheritance has been studied.

1. Inheritance of Mental Disorders. Spinal ataxia is a condition in which the sensory nerve tracts degenerate, cutting off the sensory impulses on which equilibrium depends. A person suffering from this cannot stand without swaying, and in the advanced stages loses all power of independent movement. The condition is inherited through a recessive factor in some families, through a dominant one in others.

A single, dominant gene causes the degeneration of the large ganglion cells of the floor of the cerebrum, which results in involuntary movements, especially of the hands—a condition known as **paralysis agitans.**

Another dominant factor, causing involuntary twitchings of the head, arms and legs, and known as **Huntington's chorea,** appears only after maturity. The condition becomes progressively worse, leading to insanity and death. Almost all the cases of this disease in the United States can be traced back to three brothers who landed in New England in the seventeenth century.

Juvenile amaurotic idiocy, a defect which appears within the first two years of life, is inherited through a single, recessive gene. The disease is characterized by the degeneration of the nervous system and the retina of the eye, and results in blindness, paralysis, mental failure and death.

Phenylketonuria, a type of imbecility caused by a single, recessive gene, is accompanied by the excretion of a substance known as phenylpyruvic acid into the urine. The gene blocks a certain chemical reaction with the result that phenylpyruvic acid—normally oxidized by a series of steps to carbon dioxide and water, and hence absent from normal urine—accumulates in the blood and is excreted in the urine. The connection between this chemical block and the imbecility is not understood.

The method of inheritance of some of the other types of mental disorders is more obscure. The commonest type of insanity is **dementia praecox,** in which the patient lives in a world of his own. Losing interest

in the normal pattern of life, he becomes withdrawn and incoherent. The disease definitely runs in families and apparently is brought about by the interaction of several pairs of recessive genes. Clear evidence of its hereditary nature comes from studies of twins. In identical twins, where the hereditary factors are identical, if one member of the pair has dementia praecox, the other shows it in a large percentage of cases (68 per cent according to one report). Environmental differences affecting the penetrance of the genes are responsible for the absence of the disorder in the remainder of the cases. In fraternal twins, where the hereditary factors are no more similar than in ordinary brothers and sisters, the second member of the pair develops dementia praecox in a much smaller percentage of cases (15 per cent according to the same study). This method of comparing identical and fraternal twins is an important tool for determining whether a given condition has a hereditary basis. A committee of the American Neurological Association has examined studies made by various investigators and concluded that heredity plays an important part in producing dementia praecox, but that hereditary factors are sometimes inadequate by themselves to produce the disease. And it may even appear in the absence of such factors, so that they are not invariably essential.

Manic-depressive insanity is a type in which the individual is abnormally sensitive to his surroundings and undergoes exaggerated changes of mood from the manic (excited) to the depressive state. Again, studies of twins show that hereditary factors are involved. In identical twins, if one member of the pair exhibits this type of insanity, the other member does also in a high percentage of cases (70 to 96 per cent in different studies). As for fraternal twins, only in a minority of pairs do both members have the condition (7 to 14 per cent according to different investigators). Family histories of manic-depressive insanity indicate that several pairs of genes are active, some of which are dominant.

Epilepsy, in which a person suffers from periodic convulsions and loss of consciousness, may be caused either by genetic factors or by injury or infection of the brain. The cases caused by genetic agents seem to depend on several pairs of recessive genes. Recent work with the electroencephalograph (see p. 277) indicates that the relatives of epileptics sometimes show disordered brain waves, but not the epileptic seizures. Such people may possibly have some, but not all, the genes necessary for the manifestation of epilepsy. It is advisable that two people with such disordered brain waves, even though they do not have epilepsy, should avoid having children, because their offspring might very well be epileptics.

The genetic basis of mental ability or intelligence is one of the most important and, at the same time, one of the most difficult of all problems of human heredity. The interpretation of genetic facts can easily become colored by political, sociological, psychological or educational ideas, and it is essential for the investigator, as well as the layman, to be objective and sure of his facts before accepting or offering any theory relating to the inheritance and development of intellect.

Because of the difficulties surrounding the measurement of intelligence, some investigators deny the validity of all intelligence tests.

Within limits, however, they seem to have a definite value. The widely used tests, such as the Stanford-Binet, are prepared by setting tasks for children, and determining what capacities can be expected normally of each age. In taking the test, a child is given progressively more difficult problems until he is unable to solve one. As a result, a wide range of mental ability from complete incompetence to excellent comprehension has been found for every age group. A child of six who can solve problems ordinarily solved by children eight years old, obviously is superior to one of six who can do only those normally done by children six years old. This "mental age," as determined by the test, is divided by the actual chronological age and the quotient multiplied by 100 to give the "intelligence quotient" or **I.Q.** An I.Q. of 100 is normal. When the I.Q.'s of a large number of people are determined, they can be seen to form a normal curve of distribution from 0 to over 140, with the largest number of scores in the normal class, and progressively fewer scores in the classes farther from the normal (Table 13).

Table 13. Classification of Intelligence

I.Q.	Designation	
140 or over	"Genius"	
120–140	Very superior	
110–120	Superior	
90–110	Normal	
80– 90	Dull	
70– 80	Borderline	
50– 70	Moron	"feeble-minded"
25– 50	Imbecile	"feeble-minded"
0– 25	Idiot	"feeble-minded"

People with an I.Q. less than 70 are termed as **"feeble-minded"**, and three grades of the condition are recognized. The highest class, **morons**, includes those with an I.Q. between 50 and 70. These people are unable to govern their affairs satisfactorily, but can perform simple tasks and may be partially self-supporting. The next lowest class, **imbeciles**, includes people whose I.Q.'s are between 25 and 50, corresponding to a mental age of three to seven years. These are unable to earn a living but can take care of themselves. The lowest class, known as **idiots**, is composed of people with a mental age of one or two, or an I.Q. between 0 and 25. Idiots cannot perform even so simple a task as feeding themselves.

That the mental capacities of different people form a continuous series from idiot to genius, with the distribution of the I.Q.'s conforming to a normal curve, suggests the operation of multiple factors, and other evidence substantiates this hypothesis. Some of the early studies attempted to divide people into two classes, normal and feeble-minded, and explained the inheritance of feeble-mindedness as due to a single, recessive gene. We know now that the inheritance of this defect is much more complex, and that such reports as those of the "Jukes" and "Kallikaks" are not valid genetically.

Feeble-mindedness may be caused by diseases such as syphilis or meningitis, by injuries at birth, or by other environmental agents, but the majority of cases are due to hereditary factors. In addition to evi-

denee to this effeet from family histories, studies of twins have shown that in fraternal twins, when one twin is feeble-minded, the other one also is feeble-minded in about 25 per eent of the eases. In identieal twins, when one is feeble-minded, the other shares the trait in nearly every ease.

Superior mental ability also tends to "run in families." Some believe this to be due to heredity; others believe it is explained by better family environment and training. The environmental theory, however, would not aeeount for the notable differenees in intelligenee which oeeur within a family. Sueh differenees ean be explained, on the genetie theory, by the segregation of the various genes eoneerned.

Several studies have resulted in the following eonelusions, indieating the hereditary basis of intelligenee.

(*a*) Children reared together in an orphanage (environment similar) show just as wide variability in intelligenee as ehildren reared in their own homes.

(*b*) Where ehildren are adopted early in infaney, there is a mueh greater eorrelation between the intelligenee of the ehild and its true parents than between the ehild and its foster parents.

(*c*) Identieal twins are mueh more similar in intelligenee than fraternal twins.

(*d*) Identieal twins reared apart are more similar in intelligenee than fraternal twins reared together.

It may be eoneluded, therefore, that the upper limit of a person's mental ability is determined by hereditary faetors. But how fully he develops his inherited mental abilities is determined by environmental influences—training and experience.

It is easy to explain why the offspring of intelligent parents are sometimes less intelligent than either parent. Sinee the eoordinated aetion of many pairs of genes is involved in intelligence, the fortuitous eombination of faetors whieh produeed the intelligent parents may segregate. A new combination of genes may be set up in the offspring, resulting in lowered mental ability. Conversely, the ehanee reeombinations of favorable faetors may produee a brilliant ehild from average parents (but geniuses are never produeed by feeble-minded parents).

2. Inheritance of Special Abilities. In addition to general mental ability, eertain speeial eapaeities, sueh as musieal, artistie and meehanical talents, have a hereditary basis. Inheritanee of musieal ability has been investigated more thoroughly than the others, ehiefly beeause it ean be measured more aeeurately. Philiptsehenko studied the inheritance of this trait and found evidenee that four pairs of genes are involved. Musieal ability is a eomplex of piteh diserimination, tone memory, and a sense of rhythm, melody and harmony, so that it is not surprising that its inheritanee is eomplex. Speeial abilities are at least partially independent of general intelligenee, investigations of feeble-minded persons showing that some have marked musieal and meehanieal talents.

IV. EUGENICS

As a result of the inereasing knowledge of human inheritanee, many proposals for the seientifie improvement of man's heredity have been

made, and the science of **eugenics** is now well established. Eugenics may be negative—consisting simply in preventing the reproduction of people with undesirable hereditary traits—or positive—encouraging reproduction of those with superior hereditary characteristics. There can be no argument about the undesirability of traits such as feeble-mindedness, insanity or epilepsy, and the more appalling physical abnormalities such as ateleiropodia, in which the arms and legs are short stumps devoid of hands and feet.

The biggest single eugenic problem is feeble-mindedness, since about 5 per cent of the American population have an I.Q. of 70 or less. These folk contribute little or nothing to society, and many of them are burdens as paupers, criminals or inmates of institutions. The idiots and imbeciles usually are confined and unable to reproduce, but the morons, who constitute the majority of the class, ordinarily are not institutionalized, and commonly have more children than do normal people. This is truly deplorable, not only because the offspring also are often feeble-minded, but because the children's chances of receiving proper guidance and understanding are negligible. Then, too, the financial difficulties resulting from too many children in a home supported by a moron—who usually cannot command a high wage—bring recurring crises which the unfortunate person has not the intelligence to face. In response, he may resort to theft and other antisocial acts with dire consequences to the entire family.

Several negative methods for preventing the reproduction of the mentally unfit have been suggested. Segregation of these people in institutions would be effective but unkind, as well as prohibitively expensive. An alternative, **sterilization,** consists in a simple operation not involving the removal of any organ, but simply the cutting of the vas deferens of the male or the oviducts of the female. In no way does it alter the person's sexual desires or experiences, it simply prevents his becoming a parent. Although twenty-seven states have enacted laws providing for the sterilization of the feeble-minded, the insane or both, only in California has the program been carried out extensively. There, more than 14,000 people have been sterilized. A survey shows that the results are satisfactory both to the people sterilized and to society. Because there are no children to be supported by the low earnings of the mentally deficient couples, the marriages tend to be more permanent. The constitutionality of sterilization was settled by the Supreme Court decision rendered May 2, 1927, in which Justice Oliver Wendell Holmes, acting in Buck versus Bell, remarked, "Three generations of imbeciles are enough."

Another familiar eugenic method is **contraception,** which involves some device, mechanical or chemical, for preventing the sperm from reaching the egg. Because of legislation, the free spread of information about contraception is hindered, although the practice is much too firmly established ever to be abolished by law. For the feeble-minded it is not as effective as sterilization, because most of them are too dull or too careless to use contraceptives successfully.

Still another eugenic method, which operates almost everywhere, is the prohibition of the marriage of brothers and sisters or first cousins.

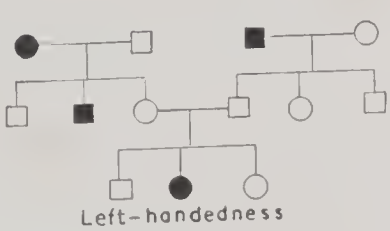
The effectiveness of negative eugenics in ridding a population of un-

desirable traits varies with the method of inheritance involved. A trait due to a single, dominant gene is the easiest to eliminate; next easiest to wipe out is one inherited by a single, sex-linked, recessive gene; next, one determined by a single, recessive gene. The most difficult to eliminate are those due to the interaction of several pairs of genes.

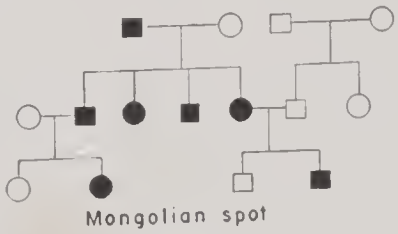
To encourage the reproduction of people with genetically desirable traits, schemes are frequently proposed involving bonuses to superior families with many children, family and educational allotments, and so forth. To date, they have been impractical, to say the least. The fact is that, regardless of what might be desirable, the number of children a couple has is largely determined (barring accidents) by their personal philosophy and disposition, which are not likely to be changed by any positive eugenic program, even of the bonus-granting variety. Indeed, except for those cases involving serious mental or physical handicaps capable of rendering any possible offspring miserable or incompetent, it seems somewhat impertinent to even suggest a course of action in regard to this matter. For on the human level it is first and foremost a personal problem, and only secondarily a social one.

QUESTIONS

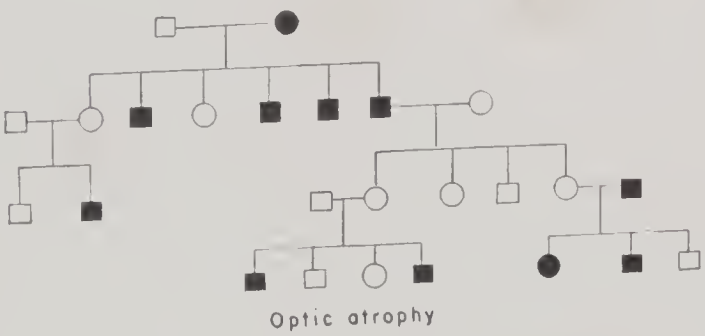
1. What difficulties are inherent in the study of human inheritance?
2. What is the difference between "congenital" and "hereditary?"
3. Discuss the statement, "If a certain disease is shown to have a hereditary basis, medical research on that disease is useless."
4. Could two dark-haired parents have a red-haired child? If so, what genotypes must the parents have?
5. What kinds of traits are easiest to eliminate by negative eugenic methods? Why are they easier to eliminate than others?
6. Is there a law in your state providing for the sterilization of the feeble-minded or the insane? If so, has it been enforced?
7. In each of the following pedigrees, determine the method of inheritance of the trait, and, as far as possible, fill in the genotypes of each individual. Assume that any individual who marries into the family and does not exhibit the trait does not carry any recessive genes for it.



Left-handedness



Mongolian spot



Optic atrophy

SUPPLEMENTARY READINGS

Gates, R. R.: *Human Genetics.* New York, The Macmillan Company, 1946.
A vast compendium of knowledge about the inheritance of normal and abnormal characteristics in man.

Holmes, S. J.: *Human Genetics and Its Social Import.* New York, McGraw-Hill Book Company, Inc., 1936.
A basic discussion of eugenics.

Muller, H. J., Little, C. C., and Snyder, L. H.: *Genetics, Medicine and Man,* Ithaca, Cornell University Press, 1947.
A nontechnical discussion of the inheritance of certain human abnormalities.

Newman, H. H.: *Multiple Human Births.* New York, Doubleday, Doran & Company, Inc., 1940.
A discussion of twinning and the evidence from fraternal and identical twins on the effects of heredity and environment in man.

Scheinfeld, A.: *You and Heredity.* New York, F. A. Stokes and Co., 1939.
A popular, readable account of the inheritance of human characteristics.

Snyder, L. H.: *Medical Genetics.* Durham, N. C., Duke University Press, 1941.
A brief description of some inherited abnormalities.

Stern, C.: *Principles of Human Genetics.* San Francisco, Wm. Freeman and Co., 1949.
A well-written, simple discussion of human genetics.

PART VII

EVOLUTION AND ADAPTATION

CHAPTER 26

PRINCIPLES AND THEORIES OF EVOLUTION

CURIOSITY concerning the origin of the universe, the world, and living things seems to be a universal characteristic of human intelligence, and in all societies, from the most primitive and isolated, to the great, far-flung civilizations, men have devised legends to appease this longing for an understanding of first causes. Of these traditional stories, remarkably alike in many details, the Book of Genesis was the one accepted by the peoples of the West for many centuries, so that, until less than a century ago, most Christians believed that the universe was created in six days some 4000 years before Christ.

Since about 1860, however, it has become increasingly clear that the earth is much older than was supposed and that it is impossible to date the beginning of the universe—if, indeed, it had a beginning. We now know that about two or two and a half billion years ago this planet came into being, either from material torn from the sun or as an aggregation of dust from interstellar space. Some time later—perhaps a billion and a half or two billion years ago—life began in some simple form. All organisms living today, including man, descended from those earliest bits of protoplasm and so are related to each other.

1. Organic Evolution. In a broad sense, evolution means unfolding or unrolling—a gradual, orderly change from one condition to another. Thus many things besides life have evolved: the planets and stars, the earth's topography, the chemical compounds of the universe, and even the chemical elements, made up of electrons, protons, neutrons and other subatomic particles. Such changes are sometimes called **inorganic evolution.**

The principle of **organic evolution,** which is simply the application of this concept to living things, states that all the various plants and animals existing at the present time have descended from simpler organisms by gradual modifications which have accumulated in successive generations.

It is important to realize that evolution has not ceased, but is occurring more rapidly today than in many of the past ages. In the last few hundred thousand years, hundreds of species of animals and plants have become extinct and other hundreds have arisen. Although the process is usually too gradual to be observed, there are notable examples of evolutionary change within the time of recorded history. For example, early in the fifteenth century a litter of rabbits was released on Porto Santo, a small island near Madeira. Since there were no other rabbits and no carnivorous enemies on the island, the rabbits multiplied with amazing speed and by the nineteenth century were strikingly different

from the ancestral European stock. They were only half as large as their European relatives, had a different color pattern, and were more nocturnal. But most important was the fact that they could not breed with members of the European species. Within four hundred years, then, a new species of rabbit had developed.

The idea that the present forms of life arose from earlier, simpler ones was not new when Darwin's *The Origin of Species* was published in 1859. Elements of the theory of organic evolution are to be found in the writings of the early Greek philosophers, Thales (624–548 B.C.), Anaximenes (588–524 B.C.), Empedocles (495–435 B.C.) and Epicurus (341–270 B.C.). Aristotle (384–322 B.C.), who was a great biologist as well as a philosopher, worked out an elaborate theory of gradually evolving life forms, according to the metaphysical belief that nature strives to change from the simple and imperfect to the more complex and perfect. The Roman poet Lucretius (99–55 B.C.) also gave an evolutionary explanation of the origin of plants and animals in his poem *De Rerum Natura*. Under the Church's domination of philosophy, during the Dark and Middle Ages, the theory was not developed, but with the Renaissance, interest in the natural sciences revived, and from the fourteenth century on an increasingly large number of people found the concept of organic evolution reasonable. In *The Origin of Species* Darwin lists about twenty thinkers who had considered the theory seriously, among them his own grandfather, Erasmus Darwin (1731–1802), and the French scientist Lamarck (1744–1829).

Long before the Renaissance, in many different places, men had discovered odd fragments resembling bones, teeth and shells. Some of these corresponded to parts of familiar, living animals, but others were strangely unlike any known form. An especially puzzling factor was that many of the objects found in rocks high in the mountains resembled parts of marine animals. Leonardo da Vinci, in the fifteenth century, correctly interpreted these curious finds, and gradually people accepted his explanation that they were the remains of once-existing animals that had become extinct. Such evidence of former life suggested the theory of **catastrophism**, which stated that, since the world began, a number of fires and floods periodically have destroyed all living things and necessitated the repopulation of the world by acts of special creation.

In the eighteenth century three English scientists, dissatisfied with the theory of catastrophism, proposed the scientific theory, accepted today, called **uniformitarianism**. James Hutton, in 1785, developed the concept that the geological forces at work in the past were the same as those of the present. He arrived at this conclusion after a careful study of the erosion of valleys by rivers, and the formation of sedimentary deposits at the river mouths. He demonstrated that such processes, over long periods of time, could account for the formation of the fossil-bearing rock strata. In 1802 John Playfair's *Illustrations of the Huttonian Theory of the Earth* was published, in which he gave further explanation and examples of the idea of uniformitarianism in geological processes. Sir Charles Lyell, one of the most influential geologists of his time, did much in his *Principles of Geology* (1832) to establish the principle of uniformity. By demonstrating the validity of geologic evo-

lution he proved irrefutably that the earth is much older than a few thousand years, old enough for the processes of organic evolution to have occurred. He was a close personal friend of Darwin's, with great influence on his thinking, and through his work he paved the way for, and made possible the ideas presented in, *The Origin of Species*.

2. Jean Baptiste de Lamarck. Earliest of the modern theories of organic evolution to be logically developed was that of Jean Baptiste de Lamarck, the great French zoologist whose *Philosophie Zoologique* was published in 1809. Lamarck, like most biologists of his time, was a vitalist: he believed that organisms are guided through their lives by an innate and mysterious force which enables them to overcome handicaps in the environment. He believed too that these adaptations once made are transmitted from generation to generation—that is, that acquired characteristics are inherited. Developing the notion that new organs arise in response to demands of the environment, he went on to state that their size is proportional to their "use or disuse," and that changes in size also pass to successive generations. To illustrate this, Lamarck explained the evolution of the giraffe's long neck by suggesting that an ancestor took to browsing on the leaves of trees, instead of on grass, and in reaching up, stretched and elongated its neck; its offspring then supposedly inherited the longer neck.

The Lamarckian theory nicely explains the complete adaptation of many plants and animals to the environment, but it is unacceptable because overwhelming genetic evidence indicates that *acquired characteristics cannot be inherited*. Many experiments have been performed in an attempt to demonstrate the inheritance of acquired traits, but all have ended in failure. From what we now know about the mechanism of heredity, it is obvious even without experimental evidence, that acquired traits cannot be inherited, for such characteristics are in the *body* cells only, whereas an inherited trait is transmitted by the *gametes*—the eggs and sperm.

3. Background for *The Origin of Species*. Darwin's contribution to the body of scientific knowledge was twofold: he presented a mass of detailed evidence and cogent argument to prove that organic evolution has occurred, and he devised a theory—that of natural selection—to explain how it operates.

Although his university training was in theology, Darwin was extremely interested in both biology and geology, and, while at Cambridge, became acquainted with Professor Henslow, the naturalist. Through him, shortly after leaving college, Darwin was appointed to the position of naturalist on the ship *Beagle*, which was to make a five year cruise around the world so that oceanographic charts could be made for the British navy. Darwin studied the animals, plants and geological formations of the East and West coasts of South America, making extensive collections and notes. The *Beagle* then went to the Galapagos Islands, west of Ecuador, where Darwin continued his observations of the flora and fauna, comparing them to the ones on the South American mainland. It was these observations which led him to reject the theory of special creation.

According to his journal, the idea of natural selection occurred to

Darwin shortly after his return to England in 1833, but he spent the next twenty years or so accumulating the vast body of facts which eventually became *The Origin of Species*. In 1858 he received a manuscript from Alfred Russell Wallace, a young naturalist who was studying the distribution of plants and animals in the East Indies and the Malay Peninsula. Wallace set forth in this paper the idea of natural selection, which he had reached independently, stimulated, as Darwin had been, by Malthus' book on population growth and pressure, and the struggle for existence. By mutual agreement, Darwin and Wallace presented a joint paper on their theory at the meeting of the Linnean Society in London in 1858, and Darwin's monumental work was published the next year.

4. The Theory of Natural Selection. Darwin s explanation for the way in which evolution takes place can be summarized as follows:

1. Variation is characteristic of every group of animals and plants, and there are many ways in which organisms differ. (Darwin did not know the cause of variation, and assumed it was one of the innate properties of protoplasm. We now know that variations are produced by mutations.)

2. More organisms of each kind are born than can possibly obtain food and survive. Yet, since, the number of each species remains fairly constant under natural conditions, it must be assumed that most of the offspring in each generation perish. If all the offspring of any species remained alive and reproduced, the earth would soon be filled with nothing but that species.

3. Since more individuals are born than can survive, there is a struggle for survival, a competition for food and space. This contest may be active—an eat-or-be-eaten sort of business—or passive—a not immediately apparent process, such as the struggle of plants to survive drought or cold.

4. Of the many variations exhibited by living things, some make it easier to survive in the struggle for existence, while others cause their owners to be eliminated. This idea of "the survival of the fittest" is the core of natural selection.

5. The surviving individuals will give rise to the next generation, and in this way the "successful" variations are transmitted to the next generation, and the next.

By this process each successive generation becomes better adapted to its environment, and with the changing environment, further adaptations follow. As natural selection continues to operate over many years, later descendents may be quite different from their ancestors, different enough to be a separate species. Furthermore, certain members of a population with one group of variations may become adapted to environmental changes in one way, while other members, with a different set of variations, may become adapted in a different way, so that two or more species may arise from a single ancestral species.

Animals and plants exhibit many variations which are neither a help nor a hindrance to them; these will not be affected directly by natural selection, but, of course, will be transmitted to succeeding generations.

Darwin's theory of natural selection was so reasonable and well sup-

ported that most biologists soon accepted it. But along with its great success it encountered certain criticisms, most of which were satisfactorily answered when more about the hereditary mechanism was discovered. One of the early objections was that the theory did not explain the appearance of many apparently useless structures in an organism. It is now known that many of the visible differences between species are not important for survival, but are simply incidental effects of genes that have invisible, physiological effects of great survival value. Sometimes the visible differences are due to genes closely linked in the chromosome to other genes controlling characteristics important for survival.

Another objection was that new variations would be lost by "dilution" as the individuals showing them bred with others without them. We now know that genes are not "diluted" or altered* when combined with others, but emerge unchanged in succeeding generations.

5. Modern Changes in the Theory of Natural Selection. Rediscovery of Mendel's laws in 1900 made necessary two significant corrections of Darwin's theory of natural selection. The first of these states that only *inherited* variations can provide the raw material for natural selection. The second states that there must be geographic or genetic *isolation* of incipient species to prevent interbreeding.

Modifications and Mutations. Darwin did not recognize that the variations of living things have their roots in one of two sources: some (physical or chemical) action of the environment on the developing embryo, or some alteration of the hereditary materials—the genes or chromosomes. Variations resulting from the first of these two situations—called **modifications**—are not inheritable and are not significant for evolution, but variations arising from changes in the genes or chromosomes—called **mutations**—are the raw materials for evolution by natural selection. Obviously, then, evolution cannot take place without mutations, and although natural selection does not create new characteristics, it plays an important part in determining which of them shall survive.

Isolation. Darwin realized that for a new species to come into existence a group of individuals must be differentiated from others of their kind by the accumulation of new characteristics, but just as he did not understand the significance of heredity in the process, so he overlooked another important factor—**isolation.** It is now well established that for a group to become differentiated, the organisms must first be prevented from breeding with their relatives and so passing on to them whatever new genes may have appeared. The only way to prevent interbreeding is by some form of isolation.

Perhaps the most common type of isolation is *geographic,* whereby groups of related organisms become separated by some physical barrier such as a sea, mountain, desert, glacier or river. In mountainous regions the individual ranges provide effective barriers between the valleys, and there are usually more different species for a given area than on the plains. In the mountains of western United States twenty-three species and subspecies of rabbits are known, while in the larger plains area of the

* The *phenotypic expression* of a gene may be altered when it is in combination with others, but the fundamental nature of the gene itself is not changed.

Midwest and East there are only eight species. Valleys only a short distance apart, but separated by ridges perpetually covered with snow, have species of plants and animals peculiar to them. One of the most striking examples of geographic isolation is provided by the area divided by the Isthmus of Panama. On either side of the Isthmus, in general, the phyla and classes of marine invertebrates are made up of different, but closely related species—a situation brought about by the fact that for some 16,000,000 years, during the Tertiary period, there was no connection between North and South America. This made it possible for animals to migrate freely between what is now the Gulf of Mexico and the Pacific Ocean. With the emergence of the Isthmus of Panama the closely related groups of animals were isolated, and the differences between the two fauna today represent the accumulation of hereditary differences.

Geographic isolation is usually not permanent; hence two previously isolated groups may come into contact again and interbreed unless *genetic isolation* or sterility has arisen in the meantime. The various races of man are the result of isolation and the accumulation of chance mutations, but since interracial sterility has not developed, the differences begin to disappear rapidly when geographic isolation breaks down. That they do not disappear even more quickly and completely is due largely to social taboos against intermarriage—itself a form of isolation.

Because genetic sterility is due to one or more mutations occurring by chance, independently of other mutations, it may arise only after long geographic isolation has produced marked differences between two groups of organisms, or it may arise within a single, otherwise homogeneous group. Such a mutation occurred in a species of fruit fly, *Drosophila pseudoobscura,* producing two groups of flies, externally indistinguishable, yet completely sterile when mated with each other. The two groups are isolated as effectively as if they lived on different continents, and as generations pass and different mutations accumulate by chance and selection, undoubtedly they will become visibly different. Biologists usually do not consider two closely related but different groups of organsims to be different species unless this genetic isolation has arisen.

Another type of isolation, called *ecological,* depends upon the fact that two groups of animals living in the same geographical area may occupy different "niches" or habitats. Marine animals living only in the intertidal zone are effectively isolated from others living only a few feet away, below the low-tide mark. Or ecological isolation may be due to the fact that two groups breed at different times of the year.

Darwin originally assumed that in any group the variation of a particular character would continue, so that natural selection would operate indefinitely. But from the facts of heredity presented previously it should be clear that selection can operate only until the group becomes homozygous for the genes for that trait—for example, large body size. After that condition has been reached, selection can do no more until further mutations for large body size have occurred.

It must be emphasized that natural selection operates upon the organism as a whole, rather than on individual traits. Thus a given form

may survive despite obviously disadvantageous characters, while another may be eliminated despite traits extremely advantageous for getting along in life. The animals and plants that win the struggle for existence are usually not perfectly adapted to their environment, but have qualities the sum total of which renders them a little better able to survive and reproduce than are their competitors. But since the environment itself changes from time to time, a characteristic of adaptive value at one period may be useless or even detrimental at another.

Chance, as well as natural selection, plays a part in determining whether a new trait will be passed from the single individual having it to the members of the group as a whole. For during the process of meiosis the gene responsible for the character may or may not be included in the gametes; and even if it is included, a series of unlucky accidents may eliminate the few, early organisms having it, so that in spite of high survival value it disappears.

6. Preadaptation. One of the recent modifications of the theory of natural selection, which answers a number of the objections leveled against the original theory and accounts for the evolution of such things as vestigial organs, is the theory of **preadaptation.** Because mutations occur at random, some result in characteristics either unimportant or disadvantageous to the organism in its usual environment. If, however, the environment changes or the organism migrates to a new location, these same traits may be of marked value for survival. That is, an animal or plant may be adapted to an environment before being exposed to it. Suppose that a mutation in a fish occurs causing both eyes to be on one side of the skull. Obviously, if the fish continues its old habits, such a formation will be a handicap. But if the animal takes to lying on its side on the bottom of the sea and grubbing in the mud for food, the new arrangement will be advantageous. This mutation actually has occurred in the flounder.

Preadaptation reasonably explains such occurrences as the evolution of land forms. For example, in a species of fish inhabiting a lake or river of the Devonian period, some 350,000,000 years ago, mutations may have occurred for the formation of primitive lungs and for changing the fan-shaped fins to sturdier, limb-like fins with a fleshy lobe at the base. Such changes would have had no survival value for the fish and might have been deleterious—by forcing it to swim more slowly—as long as it lived in a lake or stream. But the Devonian age was one of violent climatic changes, in which seasons of drought alternated with seasons of rain. As the streams dried up, the water became stagnant and lacked sufficient dissolved oxygen for gills to function in respiration. An animal with lungs, however, could come to the surface, take a gulp of air, and obtain oxygen by diffusion across the membrane lining the lungs. Then, when the pond or stream dried up completely, he could use his sturdy, lobe-shaped fins to walk across the intervening land to some other stream. By some such process the evolutionary conquest of the land probably occurred. Certainly the first animals to venture out of the water onto land were not seeking air, for their ancestors already had lungs and could get air by coming to the surface; nor were they fleeing predators, for they were among the largest animals alive at the time. Since they ate other

fish, and the only food on land was insects and plants, it can hardly be supposed that they were seeking food. Paradoxically, the first animals to come out on land were probably looking for water, their own pond having just dried up.

7. Mutation Theory of de Vries. The Dutch botanist Hugo de Vries, one of the three rediscoverers of Mendel's laws, was the first to emphasize the importance in evolution of sudden, large changes rather than the gradual accumulation of many small changes postulated by Darwin. De Vries experimented with a number of plants, especially the evening primrose, which grew wild in Holland. When he transplanted these plants into his garden and bred them, he found that many unusual forms, differing markedly from the original wild plant, appeared and bred true thereafter. For these sudden changes in the characters of an organism (which had been called "sports" by earlier breeders) he coined the name **"mutation."** Darwin had referred to a number of such changes, but believed that they occurred too rarely to be important in evolution, and that they might upset the harmonious relations between the various parts of the organism, and its adaptation to the environment. Countless breeding experiments on all kinds of plants and animals since 1900 have shown that such mutations occur constantly and that their effects are often not lethal. With the development of the theory that the hereditary materials are the genes, located in the chromosomes, the term "mutation" has come to refer to sudden, discontinuous, random changes in the genes and chromosomes, although it is still used to some extent to refer to the new type of plant or animal.

In the plants and animals most widely used in breeding experiments—corn and fruit flies—some 400 and 600 mutations, respectively, have occurred within the past forty years. The fruit fly mutations are tremendously varied, including all shades of body color from yellow through brown and gray to black; red, white, brown or purple eyes; peculiarly shaped wings (crumpled, curled or shortened) and a complete absence of wings; oddly shaped legs and bristles; and such extraordinary arrangements as a pair of legs growing from the forehead in place of the antennae (Fig. 214). Among domestic animals, mutations are no less common; the six-toed cats of Cape Cod and the short-legged breed of Ancon sheep are two of many examples of the persistence of a single mutation. Short legs were useful to the breeder for preventing the sheep from leaping over fences; hence the trait was selected for in breeding.

Early in the present century a heated discussion arose as to whether evolution is due to natural selection or to mutations. Then, as more was learned about heredity, it became clear that natural selection can operate only when there is something to be selected—in other words, when mutations present alternate ways of coping with the environment. The evolution of new species, then, involves both mutation and natural selection.

A similar argument has continued to the present day between the Neo-Darwinists, who believe that new species evolve by the gradual accumulation of small mutations, and another group, who believe that new species and genera arise in one step by a **macromutation** or major

change in the genetic system. Such a macromutation, by producing a major change early in embryological development, is believed by the latter group to result in an adult form vastly different from its parents —the new species or genus. Many major changes result only in mon-

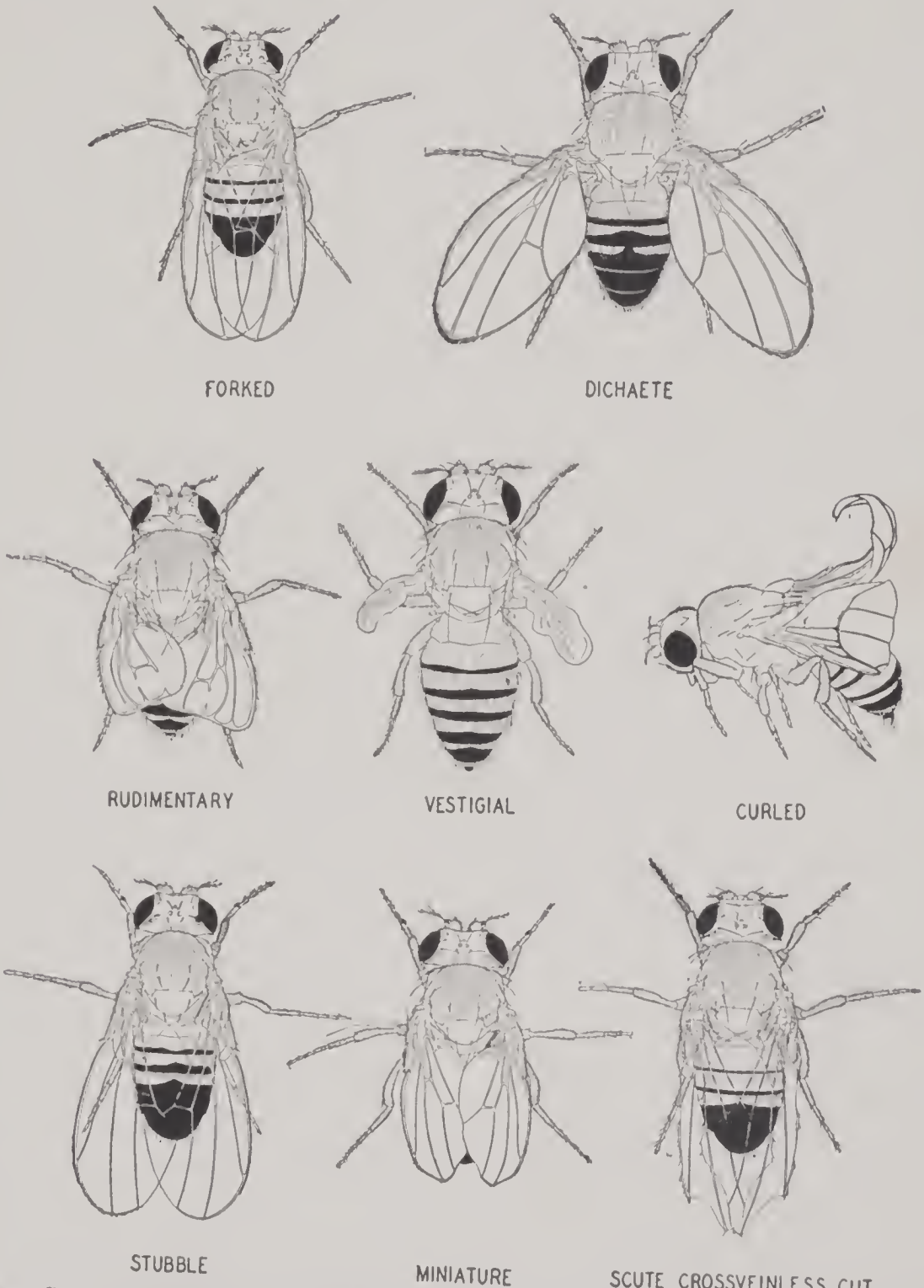


Fig. 214. Some wing and bristle mutants in the fruit fly, *Drosophila melanogaster.* (Drawn by E. M. Wallace; from Sturtevant and Beadle: An Introduction to Genetics.)

sters,* which die almost immediately, though some give rise to what Professor Goldschmidt of the University of California calls "hopeful monsters"—forms enabled by their mutation to occupy some new environment. Such a situation, he thinks, is responsible for the evolution

* The term "monster" refers to any form which departs markedly in structure from the usual type of the species, and does not necessarily imply ugliness.

of the extinct ancestral bird, *Archaeopteryx,* into the modern bird. The *Archaeopteryx* had a long, reptile-like (though feathered) tail; if, by a single mutation, that tail was greatly shortened, a "hopeful monster" with the fan-shaped arrangement of feathers might well have been the result. The new tail, then, which was better suited for flying than the old, long one, might have been selected for until, today, all birds have fan-shaped tails. There is, of course, no proof that this is how our present-day birds evolved, but there is much evidence that similar large skeletal changes do occur as the result of a single mutation. The Manx cat, for example, owes its stubby tail to a mutation in some ancestor, which caused the shortening and fusing of the tail vertebrae. Goldschmidt does not deny the accumulation of small mutations, but holds that they can lead only to varieties or geographic races and not to species, genera and the higher taxonomic divisions.

8. Types of Mutations: *Gene Mutations.* There are two types of mutation; one of them, **gene mutation,** involves changes in the chemical or physical constitution of a chromosome at some *particular point* where a certain gene is located. Although the chemical nature of genes is unknown, they are believed to be large molecules of protein or nucleoprotein. Hence gene mutations are thought to be changes in the arrangement of the atoms constituting this molecule, which alter its chemical activities and bring about a new phenotypic expression of the gene. This type of mutation is accompanied by no change in the chromosome visible under the microscope.

Chromosome Mutations. The second kind of change, chromosome mutation, involves alterations in the number of chromosomes or in the visible structure of some chromosome. There may be an addition or subtraction of a single chromosome from the usual diploid set, or there may be a doubling or tripling of the entire set, producing organisms called **polyploids,** which are usually larger and more robust than their parents. Such changes in chromosome number are more frequent in plants than in animals, because, owing to the nature of the reproductive process in plants, there is a greater chance of their being passed from one generation to the next. Some of the cultivated varieties of tomatoes, corn and other plants owe their vigor and the large size of their fruit to the fact that they are polyploids.

Changes which may occur in the visible structure of a chromosome are the deletion of a small part, doubling of a small part, and the inverting (turning end for end) of a small or large section. Sometimes there is an interchange of segments, called a translocation, between two different chromosomes. Each of these changes may produce phenotypic changes and may be inherited in a mendelian fashion. In fact, many traits previously thought to be inherited by true genes have been found to arise from chromosome mutations. This has led some geneticists to conclude that there are no genes in the sense of individual structures in the chromosome, but that the factors called genes are really chromosome mutations.

9. Frequency of Mutations. Mutations occur naturally with much greater frequency than one might expect from the relative stability of wild species and the rarity of mutant phenotypes in nature. Different

species vary widely in the rate at which mutations occur spontaneously; furthermore, there appear to be genes which govern the rate at which other genes mutate. With the aid of certain genetic techniques an estimate can be made of the frequency of mutations in a population. It is estimated that there is one new mutation in every 150 fruit flies, and that in some plants as many as 5 to 10 per cent of the offspring have a new mutation of at least one gene. These mutations are not simply laboratory freaks, as some investigators have claimed, for when wild populations of animals, such as the fruit fly, are analyzed genetically, they are found to have many mutant genes.

10. Causes of Mutations. The causes of natural or spontaneous mutations are unknown, although both gene and chromosome mutations can be produced artificially by a variety of agents: x-rays; the alpha, beta and gamma rays emitted by radioactive elements; neutrons, heat and cold; ultraviolet rays; chemicals, such as the war gas known as nitrogen mustard; and, in plants, the aging of seed. Cosmic and other rays present in the environment may cause some natural mutations. But since the genes are believed to be complex, unstable molecules, it is possible that metabolic processes in the cell bring about some spontaneous mutations, without the intervention of external agents.

Whatever their cause, the role of mutations as the raw material for natural selection and evolution is now universally recognized. It was formerly argued that the mutations observed in the laboratory have nothing to do with evolution, because (1) almost all are detrimental, and (2) the differences between species are usually slight variations, affecting many different parts of the organism and inherited by means of multiple factors, whereas the mutations observed in the laboratory are usually large variations, involving a single organ and inherited by single gene differences. The answer to the first objection is that in wild populations, as in the laboratory stocks, mutations at the present time are usually detrimental. The animals and plants living today are the result of a long process of natural selection which preserved the most beneficial mutations; they are, therefore, highly specialized and well adapted to their environment, and further mutations are disadvantageous rather than helpful. A few laboratory mutations are beneficial and have survival value.

The second objection has been eliminated by further observation which showed that the slight variations differentiating species do appear in the laboratory, but, being difficult to detect, were missed in some of the earlier work. Indeed, we now know that the rate of such mutations is greater than that of the larger, more obvious ones.

11. Straight-Line Evolution. One interesting phenomenon in the evolutionary process is the occurrence of what is called straight-line evolution, in which a series of animals form a continuous, progressive line between two different forms. A classical example of this is the evolution of the modern horse from *Eohippus*, a small, four-toed animal the size of a fox, which lived some 55,000,000 years ago (Fig. 215). In the increase of size, alteration of the size and structure of the teeth, and the reduction of the number of toes, this evolutionary development is marked by what appears to be a straight line, for all the intermediate

forms are intermediate in these characters and can be assembled in a graded series.

Superficially similar to straight-line evolution, and sometimes given the same label, is a process involving the overdevelopment of a particular characteristic. Thus, in some species, certain organs have developed so far beyond the point of usefulness as to lead to the extinction of the group. An illustration of this is the evolution of antlers in the now extinct Irish deer. With each generation the antlers became larger, and although at first this was helpful, the organs eventually became so huge —with a spread of 11 feet—that the deer could not support them. Another example is the Jefferson mammoth, with tusks which ultimately measured 8 feet in length and weighed more than 1000 pounds apiece.

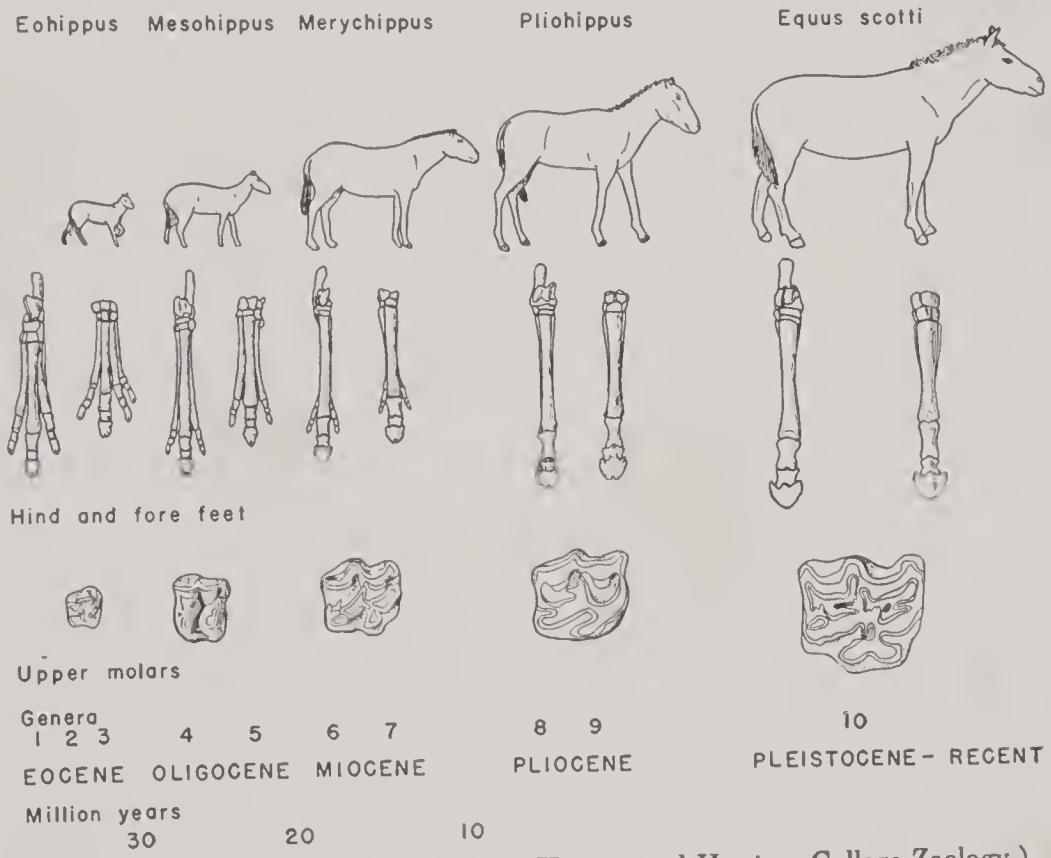


Fig. 215. The evolution of the horse. (Hunter and Hunter: College Zoology.)

Some present-day animals, too, have overdeveloped parts; the tremendous horns of the "big-horn" sheep and the long, curved tusks of wild boars are too large to be useful to the animals.

To explain both overdevelopment and straight-line evolution, many investigators, especially paleontologists, proposed a theory called **orthogenesis,** which stated that certain organisms have an inherent tendency to evolve in a definite, predetermined direction. There is no experimental evidence from genetics, however, that mutations tend to occur in a directed series, and much evidence that they occur simply at random. As more has been learned of how genes operate in controlling development, it has been possible to explain these straight-line evolutionary series within the framework of random mutation and selection. For although, by random mutation, many different alterations in the pattern of development may arise, most of them result in unharmonious patterns causing the death of the organism. Others result in changes of no par-

ticular value for survival and remain or are eliminated by chance. The ones most likely to survive are those which modify additionally some peculiar, adaptive structure the organism already has. Thus straight-line evolutionary series are the result of random mutation and selection taking place along one of the few possible lines of development. It now seems evident, too, why certain structures become too large and result in the extinction of the species. For we know that genes do not function independently, but must operate against the background of many other genes. Those controlling larger tusks, for instance, function by causing the tusks to be *proportionately* larger than the rest of the body, so that if other genes cause the entire body size to increase, the tusks may become so large as to be unmanageable and, eventually, lethal to the animals possessing them.

12. The Origin of Species by Hybridization. A simpler and less spectacular way than mutation and natural selection by which species originate is through simple hybridization or the crossing of two different varieties or species.* Through such a mating the best characters of each of the original species may be combined into a single form, thereby creating a new type better able to survive than either of its parents. Animal and plant breeders routinely use this method of obtaining new combinations of desirable characters.

When different species are crossed—ones with different chromosome numbers, for example—the offspring are usually sterile, for since the unlike chromosomes cannot pair properly in the process of meiosis, the resulting eggs and sperm do not receive the right assortment of chromosomes. But if, in such interspecific hybrids, a chromosome mutation results in the doubling of the chromosome number, meiosis can occur normally, normal, fertile eggs and sperm are produced, and the new hybrid type breeds true thereafter. Many related species of higher plants have chromosome numbers which are multiples of some basic number: there are species of wheat with fourteen, twenty-eight and forty-two chromosomes, species of roses with fourteen, twenty-eight, forty-two and fifty-six chromosomes, and species of violets with every multiple of six from twelve to fifty-four.

Evidence that such natural series probably arose by hybridization and chromosome doubling is supplied by laboratory experiments which have resulted in many similar series. One of the most famous of these experimental crosses is that made by Karpechenko, who crossed the radish with the cabbage, hoping perhaps to get a plant with a cabbage top and a radish root. Although radishes and cabbages belong to different genera, both have eighteen chromosomes, and the resulting hybrid also had eighteen chromosomes—nine from its radish parent and nine from its cabbage parent. But since the radish and cabbage chromosomes were unlike, they could not pair in meiosis, and the hybrid was almost completely sterile. By chance, however, a few of the eggs and sperm formed contained all eighteen chromosomes, and a mating between two of these resulted in a plant with thirty-six chromosomes.

* In the chapter on plants we found that, generally speaking, species are not interfertile. But occasionally two different species can interbreed, a fact which makes a hard-and-fast definition of "species" difficult. A variety is a race within a species.

This new plant was fertile, for in meiosis the radish chromosomes paired and the cabbage ones paired; it exhibited some of the characteristics of each of its parents and bred true for them. Unfortunatey, it had a radish-like top and a cabbage-like root. Since it could not be crossed readily with either of its parent species, it was in effect a new species, produced by hybridization and the doubling of the chromosome number.

An interesting example of a similar occurrence in nature is provided by a species of marsh grass, *Spartina townsendi*. This type of grass first appeared about a hundred years ago in the harbor at Southampton, England, in company with two other species, *S. stricta* and *S. alterniflora*. The new species, much more vigorous than either of the others, was soon widespread, and since it was especially valuable in collecting and holding soil, was transplanted to the Dutch dikes and other parts of the world. Because it was intermediate in many characteristics between the two species with which it was first found, it was believed to have originated as a hybrid. This was confirmed by an examination of the chromosome numbers which showed *S. townsendi* to have 126 chromosomes, *S. stricta*, fifty-six, and *S. alterniflora*, seventy. There is no doubt that the new species arose by hybridization and chromosome doubling.

13. Principles of Evolution. There is a great difference of opinion among investigators as to the nature of mutations, the kind of mutations involved in evolution, and the degree to which such factors as natural selection, isolation, genetic recombination, hybridization and the size of the breeding population affect the evolution of some particular organism, but there are several fundamental facts about which they are agreed. Let us review briefly what is actually known about how evolution operates. To begin with, we found that the basis of evolution is the changes within the genes and chromosomes, that some sort of isolation is necessary for the setting up of new species, and that natural selection is involved in the survival of some, but not all, of the mutations which occur. In addition, there are four principles of evolution to which nearly all scientists subscribe:

1. Evolution occurs more rapidly at some times than at others. At the present time it is occurring rapidly, with many new forms appearing and many old ones becoming extinct.

2. Evolution does not proceed at the same rate among different types of organisms. At one extreme are the lampshells or Brachiopods, some species of which have been exactly the same for the last 500,000,000 years at least, for fossil shells found in rocks deposited at that time are identical with those of animals living today. In contrast, several species of man have appeared and become extinct in the past few hundred thousand years. In general, evolution occurs rapidly when a new species first appears, and then gradually slows down as the group becomes established.

3. New species do not evolve from the most advanced and specialized forms already living, but from relatively simple, unspecialized forms. Thus the mammals did not evolve from the large, specialized dinosaurs, but from a group of small, unspecialized reptiles.

4. Evolution is not always from the simple to the complex. There are many examples of "regressive" evolution, in which a complex form has

given rise to simpler ones. Most parasites have evolved from free-living ancestors which were more complex than the present forms; wingless birds, such as the cassowary, have descended from birds that could fly; wingless insects have evolved from winged ones; the legless snakes came from reptiles with appendages; the whale, which has no hind legs, evolved from a mammal that had two pairs of legs. These are all reflections of the fact that mutations occur at random, and not necessarily from the simple to the complex or from the imperfect to the perfect. If there is some advantage to a species in having a simpler structure, or in doing without some structure altogether, any mutations which happen to occur for such conditions will tend to accumulate by natural selection.

QUESTIONS

1. What is the theory of uniformitarianism?
2. Explain the concept of organic evolution.
3. What is wrong with Lamarck's theory of adaptation?
4. If Darwin did not originate the theory of evolution, what contributions did he make?
5. Explain the theory of natural selection.
6. What causes the variation without which evolution could not occur?
7. What is meant by survival of the fittest? Do you think it applies to human populations?
8. Why are only inherited changes important in the evolutionary process?
9. State the theory of preadaptation.
10. After a mutation has occurred, what one condition is indispensable for evolution?
11. From what you have learned of heredity and evolution, would you be inclined to follow the Neo-Darwinists or Goldschmidt, in regard to the question of how new species originate? Give your reasons for thinking as you do.
12. Differentiate between the various kinds of mutation. What factors may produce mutations?
13. Why do nearly all the mutations occurring at the present time seem to be detrimental?
14. Contrast hybridization with the other way in which new species are produced.
15. What do you think about the belief, held by many people, that the human race is becoming better and better all the time, and is gradually evolving toward an ultimate goal of physical and moral excellence? Give specific evidence for your belief.

SUPPLEMENTARY READINGS

Darwin, C.: *The Origin of Species.* Available in a number of modern reprint editions.
The classic book on evolution, well worth sampling for its clear, logical arguments for evolution.

Dobzhansky, T.: *Genetics and the Origin of Species.* 2d ed. New York, Columbia University Press, 1941.
The modern presentation of the Neodarwinian viewpoint.

Goldschmidt, R.: *The Material Basis of Evolution.* New Haven, Yale University Press, 1940.
A detailed argument, on an advanced level, for the importance of large mutations in evolution.

Osborn, H. F.: *From the Greeks to Darwin.* New York, The Macmillan Company, 1913.
An interesting history of ideas on evolution.

Simpson, G. G.: *Tempo and Mode in Evolution.* New York, Columbia University Press, 1944.
A book combining the genetic and paleontological approaches to evolution.

CHAPTER 27

THE FOSSIL EVIDENCE FOR EVOLUTION

I. PALEONTOLOGY

EVIDENCE of the life of previous ages is so abundant and diversified that a whole science, called **paleontology,** has sprung up around it, adding immeasurably to our understanding of evolution. Unfortunately, however, the fossil record is not equally clear for all the various evolutionary lines. Most plant tissues are too soft to leave fossil remains, and although there is some evidence of prmitive trees and other woody structures, the record of the early plants is incomplete. Likewise the animals which formed the most important connecting links between the phyla had soft bodies which disappeared without leaving a trace. The record is clearest, then, of the vertebrates, because of their bones, teeth and scales, although the invertebrates with shells and other hard parts left clear remains.

Most of the vertebrate fossils discovered are skeletal parts, from which it is possible to deduce the animal's posture and style of walking. From the bone scars, indicating muscle attachments, paleontologists can deduce the general position and size of the muscles and, from this, the contours of the body. On the basis of such considerations, reconstructions, probably quite accurate, are made of how the animals looked in life, in spite of the fact that such qualities as the texture and color of the fur must be guessed at.

Although bones, shells, teeth and other hard parts are the remains most commonly found, the word "fossil" refers not only to these, but to *any* impression or trace left by previously existing organisms. Footprints or other trails made in soft mud, which subsequently hardened, are another common type of fossil. From such remains one can tell something of the structure and body proportions of the animals which made them. In 1948, tracks were discovered near Pittsburgh of an amphibian from the Pennsylvanian period, some 250,000,000 years ago. That the animal moved by hopping, rather than by walking, was evident from the fact that the footprints lay opposite each other, in pairs.

An interesting and striking type of fossil is that in which the original hard parts and, more rarely, soft tissues have been replaced by minerals —a process known as **petrifaction.** The replacing minerals may be iron pyrites, silica, calcium carbonate or other substances. The petrified muscle from a shark, more than 300,000,000 years old, was so well preserved by this process that not only individual muscle fibers, but their cross striations could be observed in thin sections under the microscope.

Superficially similar to the petrified fossils, but involving a different method of mineral replacement, are **mold** and **cast** fossils. Molds were

formed by the hardening of the material surrounding the buried organism, followed by the decay and removal of the organisms by seepage of the ground water. Sometimes the molds were subsequently filled with minerals which, in turn, hardened to form casts—replicas of the original structures.

Occasionally, paleontologists are fortunate enough to find organisms frozen in the soil or ice of the far North, usually in Siberia and Alaska. Several elephants more than 25,000 years old have been found so well

Fig. 216. Two termites imbedded in amber. These insects, dating from the Middle Tertiary (about 38,000,000 years ago), have been preserved almost perfectly. (Buchsbaum, R.: Animals Without Backbones, published by University of Chicago Press. Specimen lent by A. E. Emerson; photograph by P. S. Tice.)

preserved that their flesh was eaten by dogs. Other forms—plants, insects and spiders—have been preserved in amber, a fossil resin from pine trees. Originally the resin was a sap soft enough to engulf the fragile insect and penetrate every part; then it gradually hardened, preserving the animal intact (Fig. 216).

The formation and preservation of a fossil require that some structure be buried. This may take place at the bottom of a body of water, or on land by the accumulation of wind-blown sand, soil or volcanic ash. (Many of the men and animals living in Pompeii were preserved almost perfectly by the volcanic ash from the eruption of Vesuvius.) Sometimes animals were trapped and entombed in a bog, quicksand or

Table 14. Geologic Time Table

Era	Period	Epoch	Duration in Millions of Years	Time from Beginning of Period to Present (Millions of Years)	Geologic Conditions	Plant Life	Animal Life
Cenozoic (Age of Mammals)	Quaternary	Recent	0.025	0.025	End of last ice age; climate warmer	Decline of woody plants; rise of herbaceous ones	Age of man
		Pleistocene	1	1	Repeated glaciation; 4 ice ages	Great extinction of species	Extinction of great mammals; first human social life
	Tertiary	Pliocene	19	20	Continued rise of mountains of western North America; volcanic activity	Decline of forests; spread of grasslands; flowering plants, monocotyledons developed	Man evolved from manlike apes; elephants, horses, camels almost like modern species
		Miocene	10	30	Sierra and Cascade mountains formed; volcanic activity in northwest U. S.; climate cooler		Mammals at height of evolution; first manlike apes
		Oligocene	10	40	Lands lower; climate warmer	Maximum spread of forests; rise of monocotyledons, flowering plants	Archaic mammals extinct; rise of anthropoids; forerunners of most living genera of mammals
		Eocene	20	60	Mountains eroded; no continental seas; climate warmer		Placental mammals diversified and specialized; hoofed mammals and carnivores established
		Paleocene	5	65			Spread of archaic mammals
Rocky Mountain Revolution (Little Destruction of Fossils)							
Mesozoic (Age of Reptiles)	Cretaceous		55	120	Andes, Alps, Himalayas, Rockies formed late; earlier, inland seas and swamps; chalk, shale deposited	First monocotyledons; first oak and maple forests; gymnosperms declined	Dinosaurs reached peak, became extinct; toothed birds became extinct; first modern birds; archaic mammals common
	Jurassic		30	150	Continents fairly high; shallow seas over some of Europe and western U. S.	Increase of dicotyledons; cycads and conifers common	First toothed birds; dinosaurs larger and specialized; insectivorous marsupials
	Triassic		50	200	Continents exposed; widespread desert conditions; many land deposits	Gymnosperms dominant, declining toward end; extinction of seed ferns	First dinosaurs, pterosaurs and egg-laying mammals; extinction of primitive amphibians

Appalachian Revolution (Some Loss of Fossils)

Paleozoic (Age of Ancient Life)	Permian		15	215	Continents rose; Appalachians formed; increasing glaciation and aridity	Decline of lycopods and horsetails	Many ancient animals died out; mammal-like reptiles, modern insects arose
	Pennsylvanian		35	250	Lands at first low; great coal swamps	Great forests of seed ferns and gymnosperms	First reptiles; insects common; spread of ancient amphibians
	Mississippian		50	300	Climate warm and humid at first, cooler later as land rose	Lycopods and horsetails dominant; gymnosperms increasingly widespread	Sea lilies at height; spread of ancient sharks
	Devonian		50	350	Smaller inland seas; land higher, more arid; glaciation	First forests; land plants well established; first gymnosperms	First amphibians; lungfishes, sharks abundant
	Silurian		50	400	Extensive continental seas; lowlands increasingly arid as land rose	First definite evidence of land plants; algae dominant	Marine arachnids dominant; first (wingless) insects; rise of fishes
	Ordovician		80	480	Great submergence of land; warm climates even in Arctic	Land plants probably first appeared; marine algae abundant	First fishes, probably fresh-water; corals, trilobites abundant; diversified molluscs
	Cambrian		70	550	Lands low, climate mild; earliest rocks with abundant fossils	Marine algae	Trilobites, brachiopods dominant; most modern phyla established

Second Great Revolution (Considerable Loss of Fossils)

Proterozoic			450	1000	Great sedimentation; volcanic activity later; extensive erosion, repeated glaciations	Primitive aquatic plants—algae, fungi	Various marine protozoa; towards end, molluscs, worms, other marine invertebrates

First Great Revolution (Considerable Loss of Fossils)

Archeozoic			900	1900	Great volcanic activity; some sedimentary deposition; extensive erosion	No recognizable fossils; indirect evidence of living things from deposits of organic material in rock	

asphalt pit, such as the famous La Brea tar pits in Los Angeles which have provided superb fossils of Pleistocene animals.

II. THE GEOLOGIC TIME TABLE

Geologists have found five major rock strata, each of which is subdivided into lesser strata, and on this basis the geologic time table of eras, periods and epochs was constructed (Table 14). Some idea of the duration of each of the eras and periods is obtained from the relative thickness of the sedimentary deposits, although, obviously, the rate of deposition varied at different times and in different places.

Ideally, the layers of sedimentary rock occur in the sequence of their deposition, with the newer, later strata on top of the older, earlier ones, so that the deeper strata contain the older fossils. But often the problem of determining the relative age of rock strata is complicated by many factors. Not all the strata occur in any one region, for some lands were exposed when others were submerged; and in some localities submerged areas were subsequently reexposed, while layers previously deposited were destroyed, thereby making possible the deposition of relatively recent strata directly on top of very old ones. Moreover, certain sections of the earth's crust have undergone tremendous foldings and splittings, so that early layers may now rest on top of newer ones. Sometimes the age of a rock stratum can be determined by a study of its fossil content, for some kinds of fossils were deposited in only one era or period.

The current method of dating rocks depends on the rate of transformation of some radioactive element into another element—for example, the transformation of uranium or thorium into a distinctive kind of lead with an atomic weight different from that of ordinary lead. The rates of such transformations were essentially unaffected by the pressures and temperatures to which the elements were exposed during subsequent geologic processes. It takes 3.7 billion years for half of a given sample of uranium to be converted into lead, and, by measuring the proportion of uranium and lead in a given rock, an accurate estimate of the absolute age of the rock can be made. By this method the oldest rocks of the earliest geologic period are calculated to be about 1,850,000,000 years old, and the latest Cambrian rocks to be 450,000,000 years old.

Relatively short periods of geologic time can be determined by measuring how rapidly waterfalls are receding (Niagara Falls is moving upstream at the rate of about five feet a year, as it wears away the rock over which it tumbles) or by counting the yearly deposits of clay on the bottom of lakes and ponds. Advances in isotopic techniques have made possible some astonishing conclusions in the field of geology. For example, it has been found that the proportion of the various oxygen isotopes in the calcium carbonate secreted by living organisms depends upon the temperature; consequently, by analyzing the calcium carbonate of fossil shells, it is possible to estimate the temperature of the sea in which those animals lived, hundreds of millions of years ago.

Between the major eras widespread geological disturbances occurred, called **revolutions.** These upheavals, by raising or lowering great regions of the earth's surface and creating or eliminating shallow inland seas,

changed the distribution of sea and land organisms and wiped out many of the previous life forms. The era known as the Paleozoic ended with the revolution that raised the Appalachian mountains and, it is thought, killed all but 3 per cent of the then existing forms of life. Similarly, the Rocky Mountain Revolution, which raised the Andes, Alps and Himalayas, as well as the Rockies, resulted in the annihilation of most of the reptiles of the Mesozoic era.

III. THE GEOLOGIC ERAS

1. Archeozoic Era. The oldest of the geological eras does not begin with the origin of the earth; it dates back only to the time when the earth's crust was in solid form—that is, when rocks and mountains were already in existence and the processes of erosion and sedimentation had begun. This era, which lasted 850,000,000 to 1,000,000,000 years, was as long as all the other eras combined. Apparently it was marked by catastrophic and widespread movements of the earth, including both volcanic activity and deep-seated upheavals which climaxed in the raising of mountains. The heat, pressure, and churning associated with these movements probably destroyed most of the fossils, but some evidence of life still remains. Scattered throughout the Archeozoic rocks are traces of graphite or pure carbon, which are probably the remains of plant life, for although graphite can originate inorganically, its distribution in these rocks suggests an organic origin. What appear to be fossil algae have been found in Archeozoic rocks.

2. Proterozoic Era. The second era, some 550,000,000 years in length, was characterized by the deposition of large quantities of sediment, and by at least one great period of glaciation, during which ice sheets stretched to within 20 degrees of the equator. Sponge spicules, jellyfish and the remains of fungi, algae, brachiopods, arthropods and worm tubes have been recovered from rocks of the era.

3. Paleozoic Era. Between the strata of the late Proterozoic and the earliest layers of the third major era, the Paleozoic, is a considerable gap, caused by a geologic revolution. During the 350,000,000 years of the Paleozoic, members of every phylum and class of animals appeared except the birds and mammals. Since some of these animals existed for a relatively short time, their fossils enable geologists to correlate rocks of the same era found in different localities.

The Cambrian Period. The earliest subdivision of the Paleozoic era, the Cambrian period, is represented by rocks rich in fossils, so that the reconstructions of what the world was like in those days are probably quite accurate. The forms living in this period were so varied and complex that they must have evolved from ancestors dating back to the Proterozoic period, at the latest, and possibly to the Archeozoic. All the present-day phyla, except the chordates, were represented,* and all organisms—both plant and animal—lived in the sea. There were primitive, shrimplike crustaceans and arachnid-like forms, some of whose descendants exist almost unchanged today as the king crab. The second most numerous fossils of the Cambrian period are the brachiopods.

* It is possible that some primitive chordates did exist in the Cambrian, but with bodies too soft to be preserved.

although protozoa, sponges, gastropods, pelecypods, cephalopods and echinoderms were in existence. There were both unicellular and multicellular algae. One of the best-preserved collections of Cambrian fossils was found in the mountains of British Columbia; it includes annelids, crustacea, and a connecting link between annelids and arthropods, similar to the living peripatus.

Evolution since the Cambrian has not been marked by the establishment of entirely new body patterns, but by the ramification of the lines already present, and by the replacement of original, primitive forms with better-adapted ones. The fact that no new phyla have originated

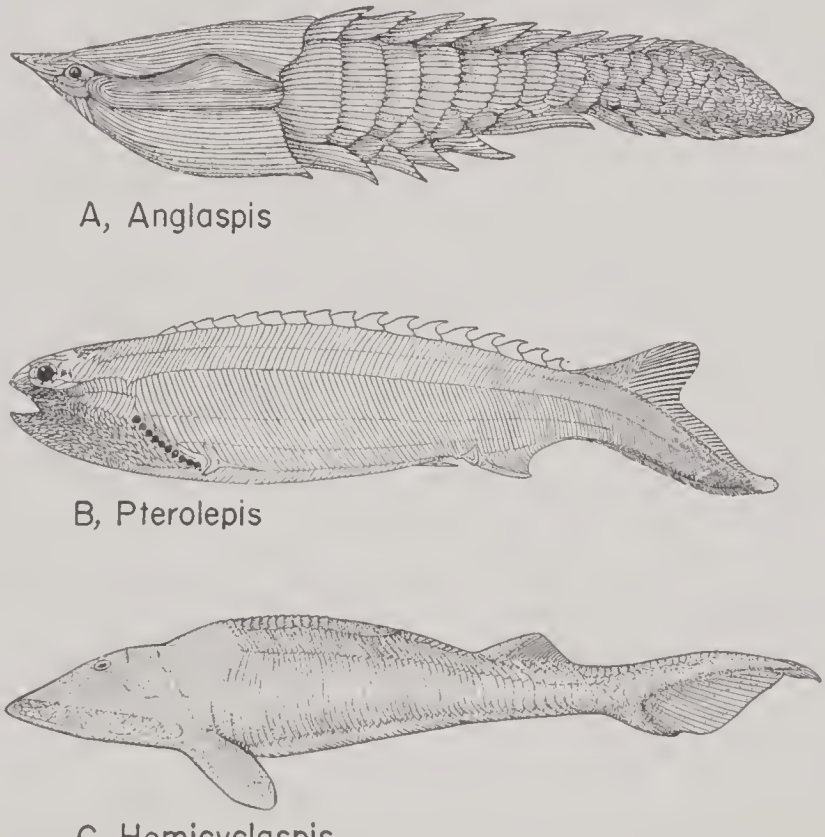


Fig. 217. Three different fossil Ostracoderms—primitive, jawless, limbless fish. (Romer, A. S.: The Vertebrate Body.)

since the early Paleozoic does not necessarily signify that no other patterns of animal organization are possible, or that mutations for new patterns did not occur. It probably indicates only that by that time the already existing forms had reached a degree of adaptation to the environment which gave them a marked advantage over any new, unadapted types.

The Ordovician Period. During the Cambrian period the continents gradually had begun to be covered with water, and in the Ordovician period this submergence reached its maximum, so that much of what is now land was covered by shallow seas. Inhabiting the seas were giant cephalopods—squid or nautilus-like animals, with straight shells, 15 to 20 feet long, and a foot in diameter. Fossil corals have been found in Ordovician, Silurian and Devonian rocks as far north as Ontario and Greenland. Since corals now grow only in warm waters, it seems likely that in those times the Northern seas were warm. The first traces of

the vertebrates are found in Ordovician rocks; these small animals, called **ostracoderms,** were jawless, armored, bottom-dwelling fishes, without fins (Fig. 217). Their armor consisted of a heavy, bony covering over the head and thick scales over the trunk and tail; otherwise they were similar to the jawless lamprey eels of today. Apparently, they lived in fresh water, and their armorplate was a defense against the carnivorous, giant water scorpions—sometimes 9 feet long—called **eurypterids,** which also inhabited fresh water.

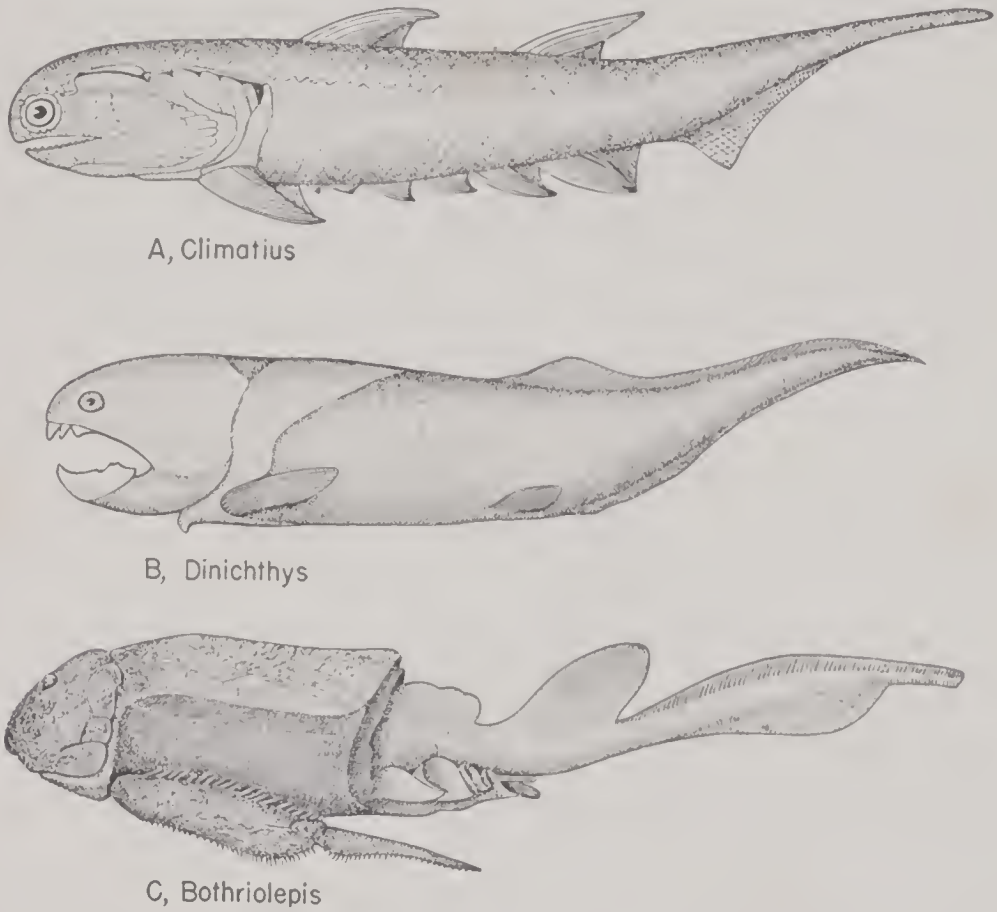
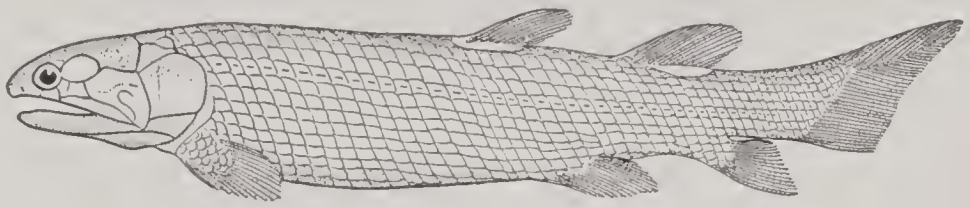


Fig. 218. Three fossil placoderms from the Devonian Period. *A*, *Climatius*, a "spiny-skinned shark," with large fin spines and five pairs of accessory fins between the pectoral and pelvic pairs. *B*, *Dinichthys*, a giant arthrodire that grew to a length of 30 feet. Its head and thorax were covered by bony armor, but the rest of the body and tail were naked. *C*, Third type of placoderm that had a single pair of jointed flippers projecting from the body. (Romer, A. S.: The Vertebrate Body.)

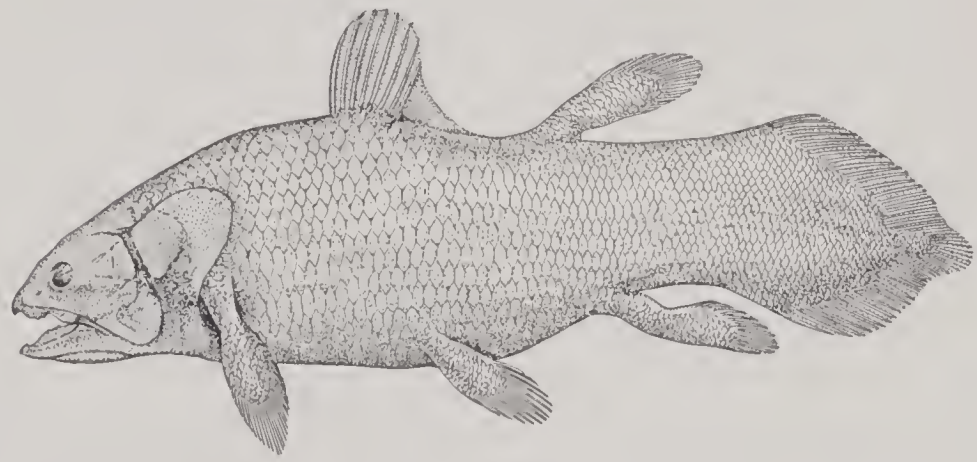
The Silurian Period. Two events of great biological importance occurred in the Silurian period: the land plants evolved, and air-breathing animals appeared. The first land plants seem to have resembled ferns rather than mosses, and ferns were the dominant plants of the following Devonian and Mississippian periods. The first air-breathing land animals were arachnids, resembling to some extent modern scorpions. The continental areas, which had been low during the Cambrian and Ordovician, rose—especially in Scotland and Northeastern North America—and the climate became much colder.

The Devonian Period. During the Devonian the original ostracoderms evolved into a great variety of fish, and the period is frequently referred to as the "age of fish." The first to evolve jaws and paired fins were the **placoderms,** or spiny-skinned sharks (Fig. 218), which were small,

armored, fresh-water forms. These animals had a variable number of paired fins; some had two, corresponding to the arms and legs of higher forms, and some had as many as five additional pairs between these two. True sharks appeared in fresh water during the Devonian, but tended to migrate to the ocean and to lose their cumbersome armorplate. The ancestors of the bony fishes* also appeared in Devonian fresh-water streams, and had evolved by the middle of the Devonian into three main types: lungfish, lobe-finned fish, and ray-finned fish. All had lungs and an armor of bony scales. A few lungfish have survived to the present, and the ray-finned fish, after undergoing a slow evolution in the remaining Paleozoic and early Mesozoic eras, ramified greatly in the latter part of the Mesozoic to give rise to the modern body fish, or



A, Osteolepis



B, Latimeria

Fig. 219. Crossopterygians. *A*, Typical fossil form from the Devonian. *B*, The living coelacanth found off Africa in 1939. (Romer, A. S.: The Vertebrate Body.)

teleosts. The lobe-finned fish, which were the ancestors of the land vertebrates, were almost extinct by the end of the Paleozoic, and it was once believed that they had vanished with the end of the Mesozoic. But in 1939 a South African fisherman pulled in an odd-looking, bluish fish, about 5 feet long, which proved to be a lobe-fin (Fig. 219).

The latter part of the Devonian was marked by the appearance of the first land vertebrates—amphibians called **stegocephalians** (meaning roof-headed) (Fig. 220). These creatures, whose skulls were encased in bony armor, were similar in most respects to the lobe-fins, differing chiefly in having limbs instead of fins. The Devonian was the first period characterized by true forests; ferns, club mosses, horsetails and primitive gymnosperms—the "seed ferns"—all flourished. Insects and millipedes are believed to have originated in the late Devonian.

* In contrast to that of bony fishes, the skeletal material of sharks is cartilage.

The Carboniferous Period. Because the greatest part of our coal deposits were made in the *Mississippian* and *Pennsylvanian* periods, these two are sometimes combined and referred to as the Carboniferous period. During this period the land was covered with low swamps, filled with horsetails, ferns, seed ferns and large-leaved evergreens (Fig. 221). The first reptiles, called **stem reptiles,** similar to their antecedent amphibians, appeared in the Pennsylvanian period, flourished in the final Paleozoic period—the Permian—and became extinct early in the Mesozoic era. It is a question whether the most primitive reptile known (called *Seymouria* for the town in Texas near which its fossil remains were found) should be considered an amphibian about to become a reptile, or a reptile just over the border from an amphibian. One of the main differences between reptiles and amphibians is the type of egg laid: amphibians lay jelly-coated eggs in the water, and reptiles lay shell-covered eggs on land. Since no Seymourian eggs have survived, it may never be possible to decide to which class this animal belonged. *Seymouria* was a large, sluggish beast resembling a lizard. Its short, stubby legs extended laterally from the body as do a salamander's, instead of being closer together and extending directly down to form a pillar-like support for the body. Two important groups of winged insects evolved during the Car-

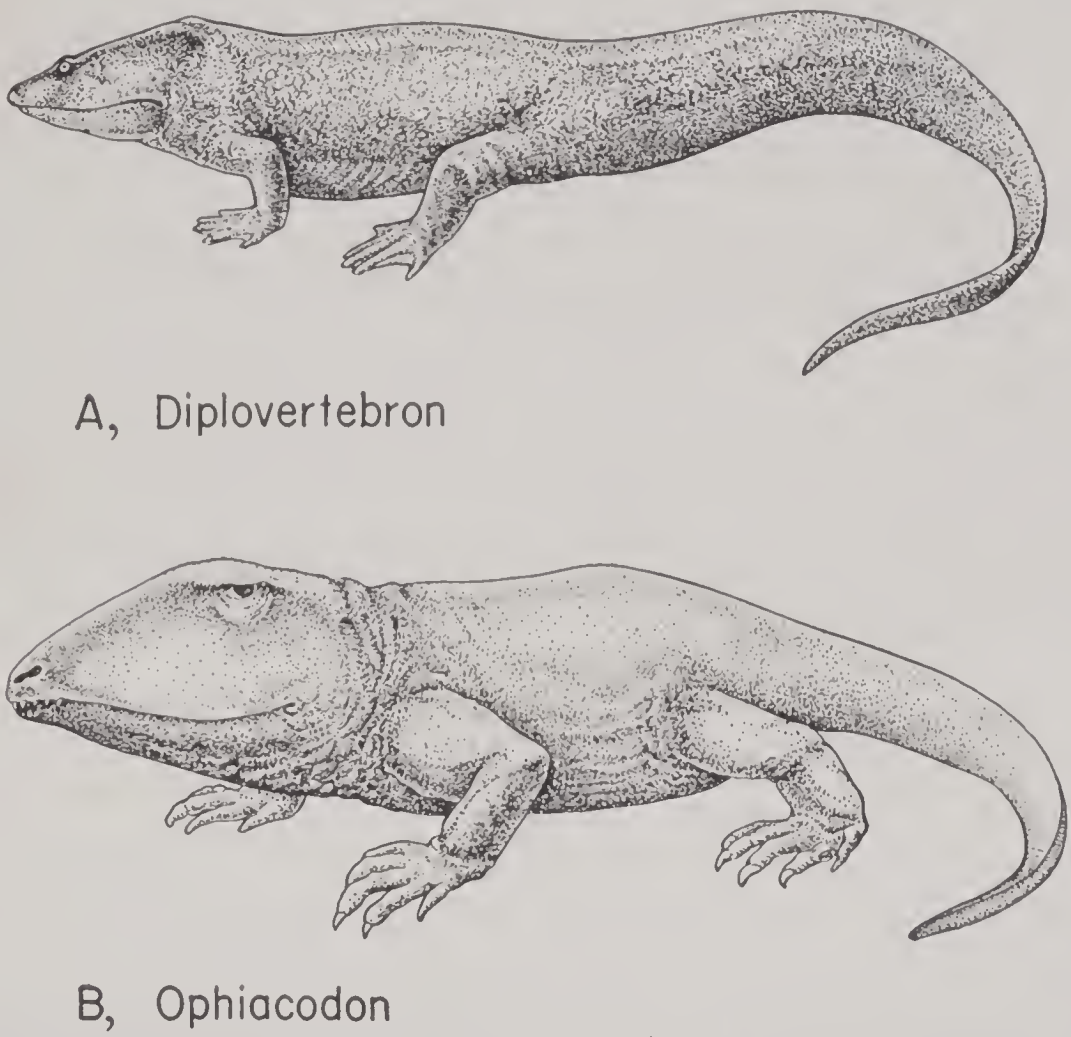


Fig. 220. *A, Diplovertebron,* a primitive Paleozoic amphibian (Stegocephalian). *B, Ophiacodon,* an early Permian pelycosaur. Although the pelycosaurs were primitive reptiles, they had certain characters indicating that they represent a first stage in the evolution of the mammals. (Romer, A. S.: The Vertebrate Body.)

Fig. 221. Restoration of a swamp forest of the Carboniferous Period. Included are giant ferns, horsetails and club mosses, primitive conifers and a large, primitive insect. (Copyright, Chicago Natural History Museum.)

Fig. 222. Texas in the Permian Period, about 215,000,000 years ago. Various pelycosaurs are shown. Some of them had large fins, others were essentially like lizards. In the right foreground are two salamander-like amphibians, with flat, horned skulls. (Copyright, Chicago Natural History Museum, from the painting by Charles R. Knight.)

boniferous—the ancestors of the cockroaches, which reached a length of 4 inches, and ancestral dragon flies, some of which had a wingspread of 2½ feet.

The Permian Period. The final period of the Paleozoic was characterized by great changes in climate and topography. The level of the continents rose all over the world, so that the shallow seas which covered the region from Nebraska to Texas at the beginning of the period, drained off, leaving the land a salt desert. At the end of the Permian a general folding of the earth's crust occurred, called the **Appalachian Revolution,** which raised the great mountain chain from Nova Scotia to Alabama. These mountains originally were higher than the present Rockies. Meanwhile, in Europe, other ranges were being brought into existence. A great glaciation, spreading from the Antarctic, covered most of the southern hemisphere, extending almost to the equator in Brazil and Africa; North America was one of the few parts of the world to escape glaciation at that time, but even its climate became much colder and drier than it had been during most of the Paleozoic. Many of the Paleozoic forms of life, apparently unable to adapt to the climatic changes, became extinct during the Appalachian Revolution. Even many

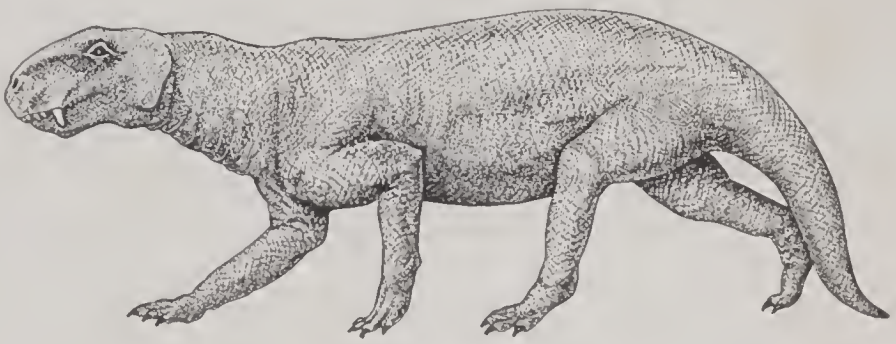


Fig. 223. A mammal-like reptile (Lycaenops) from the late Permian of South Africa. (From Romer, A. S.: The Vertebrate Body; after Colbert.)

of the marine forms became extinct, owing to the cooling of the water and the decrease in the amount of space available, caused by the diminishing of the shallow seas.

From the primitive stem reptiles there evolved during the late Carboniferous and early Permian the group of reptiles believed to be in the direct line which gave rise to the mammals. These were the **pelycosaurs** (Fig. 222), carnivorous reptiles that were more slender and lizard-like than the stem reptiles. In the latter part of the Permian there evolved, probably from the pelycosaurs, another group of reptiles with a few more mammalian characteristics—the **therapsids** (Fig. 223). One of these, *Cynognathus,* the "dog-jawed" reptile, was a slender, lightly built animal about 5 feet long, with a skull intermediate between that of a reptile and that of a mammal. The teeth, instead of being conical and all alike, as reptilian teeth are, were differentiated into incisors, canines and molars. In the absence of information about the animal's soft parts, whether it had scales or hair, whether or not it was warm blooded, and whether it suckled its young, it is called a reptile, but if more evidence were available, it might be classified as a very early mammal. The therapsids were widespread in the late Permian, but were crowded out early in the Mesozoic by the great variety of other reptiles.

4. The Mesozoic Era (The Age of Reptiles). The Mesozoic era, which began about 200,000,000 years ago and lasted some 140,000,000 years, is subdivided into three periods, the **Triassic, Jurassic** and **Cretaceous.** During the Triassic and Jurassic most of the continental areas were above water. The Triassic climate was dry, but warmer than the Permian, and the Jurassic was warmer and moister than the Triassic. The trees of the famous Petrified Forest in Arizona date from the Triassic.

During the Cretaceous period the Gulf of Mexico expanded into Texas and New Mexico, and, in general, the sea gradually encroached upon the continental areas. There were great swamps, too, from Colorado to British Columbia. In the latter part of the Cretaceous the interior of the continent of North America was further submerged, and the bay from the Gulf of Mexico, meeting another from the Arctic, cut this continent into two parts. The Cretaceous ended in another great upheaval, called the **Rocky Mountain Revolution,** which raised the Rockies, Alps, Himalayas and Andes and caused much volcanic activity in western North America.

Reptilian Evolution. The outstanding feature of the Mesozoic era was the origin, differentiation and final extinction of a great variety of reptiles, of which there were six main stocks.

The most primitive stock included, besides the ancient stem reptiles, the turtles, which originated in the Permian. The turtles have evolved the most complicated armor of any land animal, consisting of scales derived from the epidermis fused to the underlying ribs and breast bone. With this protection, both marine and land forms have survived with few structural changes since before the time of the dinosaurs. Their legs, which extend laterally, making locomotion difficult and slow, and their skulls, unpierced behind the eye sockets, have come down without alteration from the old stem reptiles.

A second group of reptiles to survive with relatively few changes from the ancestral stem reptiles, are the lizards—the most abundant of living reptiles—and the snakes. For the most part the lizards have kept the primitive type of locomotion with the legs extended laterally, although many can run rapidly. Most of them are small, but the monitor lizard of the East Indies attains a length of 12 feet, and some fossil ones are 25 feet long. The **mosasaurs** (Fig. 225) of the Cretaceous were marine lizards which reached a length of 40 feet, and had a long tail useful in swimming. During the Cretaceous, snakes evolved from lizard ancestors. The important difference between snakes and lizards is not the loss of legs (some lizards are legless), but certain changes in the skull and jaws of the snake which enable it to open its mouth wide enough to swallow an animal larger than itself. A representative of an ancient line that has managed somehow to survive in New Zealand is the lizard-like **tuatera.** It shares several traits with the ancestral cotylosaurs, one of them being a third eye on the top of its head.

The main group of Mesozoic reptiles were the **archosaurs** or "ruling reptiles," of which the only living members are the alligators and crocodiles. At an early point in their evolution from stem reptiles the ruling reptiles, which were then about 3 feet long, became adapted to two-legged locomotion—their front legs became short, while the hind legs

Fig. 224. Giant dinosaurs from the Cretaceous Period of western North America. The largest flesh-eating dinosaur known was *Tyrannosaurus*, two of which are shown attacking the herbivorous, horned dinosaur, *Triceratops*. *Tyrannosaurus* reached a length of 47 feet and a height of 19 feet. Its head was as much as 6 feet long, and equipped with many sharp teeth. The front legs were small and completely useless. It walked on its powerful hind legs and balanced with its long tail. *Triceratops* was armed with a horn on the nose and a pair of horns over the eyes and was protected by a bony ruff covering the neck and shoulders. The rest of the body was covered with a leathery hide, so that it was vulnerable except when face-to-face with its opponent. (Copyright, Chicago Natural History Museum, from the painting by Charles R. Knight.)

Fig. 225. During much of the Cretaceous Period, a shallow inland sea covered the western half of the Mississippi Valley. Three reptiles characteristic of this time and place are shown: in the center is a large mosasaur about 30 feet long; to the right is a giant, 8-foot long marine turtle; and flying in the left background are a number of reptiles of the genus *Pteranodon*, forms with short tails and a long crest extending back from the skull. (Copyright, Chicago Natural History Museum, from the painting by Charles R. Knight.)

Fig. 226. Scene off the coast of North America in Jurassic times, about 130,000,000 years ago. Two types of marine reptiles are shown: plesiosaurs with long necks, broad, flat bodies, and sturdy, paddle-shaped limbs; and ichthyosaurs with fishlike fins and tails. Both types were fish-eaters. (Copyright, Chicago Natural History Museum, from the painting by Charles R. Knight.)

Fig. 227. Western Canada in the Cretaceous Period, about 95,000,000 years ago. The land was low, well watered and covered with numerous swamps. Most of the dinosaurs were harmless, plant-eating forms of the Ornithischia group of reptiles, characterized by birdlike pelvic bones. Two types of duck-billed dinosaurs can be seen—three large, unerested ones to the right, and two types of crested ones in the left background. In the middle foreground is a heavily armored, four-footed dinosaur covered with bony plates and spines. In the center background are two ostrich dinosaurs—tall, slender animals with the general proportions of an ostrich, but with short forelegs and a long, slender tail. (Copyright, Chicago Natural History Museum, from the painting by Charles R. Knight.)

became long, stout and considerably modified. These animals rested or walked on all fours, but in emergencies they reared up and ran on the two hind legs, assisted by their fairly long tail, which served as a balance. From the early archosaurs developed many different, specialized forms, some of which continued to use two-legged locomotion, others of which reverted to walking on all fours. These descendents include the **phytosaurs**—aquatic, alligator-like reptiles, common during the Triassic; the **crocodiles,** which evolved during the Jurassic and replaced the phytosaurs as aquatic forms; and the **pterosaurs,** or flying reptiles, which included animals the size of a robin, as well as the largest animal ever to fly—*Pteranodon,* with a wingspread of 27 feet. There were two types of flying reptiles, one with a long tail that had a steering rudder at the end, the other with a short tail. Both these types, apparently, were fish eaters, and they probably flew long distances over the water in search of food. Their legs were not adapted for standing, and it is believed that, like bats, they rested by clinging to some support and hanging suspended.

Of all the reptilian branches, the most famous are the **dinosaurs** (meaning terrible reptiles). These were divided into two main types: one with a birdlike pelvis, the other with a reptilian pelvis.

The **Saurischia** (meaning reptile pelvis) first evolved in the Triassic, and remained in existence until the Cretaceous. The early ones were fast, carnivorous, two-legged forms the size of a rooster, which probably preyed upon lizards and the archaic mammals then in existence. Throughout the Jurassic and Cretaceous there was a tendency in this group to grow larger, culminating in the gigantic carnivore of the Cretaceous, *Tyrannosaurus* (Fig. 224). Other Saurischia, beginning in the late Triassic, changed to a plant diet, reverted to a four-legged gait, and, during the Jurassic and Cretaceous, evolved into tremendous amphibious forms. Among these—the largest four-footed animals that ever lived—were *Brontosaurus,* with a length of 65 feet; *Diplodocus,* which reached a length of 87 feet; and *Brachiosaurus,* the biggest of them all, with an estimated weight of 50 tons.

The other group of dinosaurs, the **Ornithischia** (meaning birdlike pelvis), were vegetarians, probably from the beginning of their evolution. Although some of them walked upright, the majority had a four-legged gait. Having lost their front teeth, they developed a stout, horny, birdlike beak, which in some forms was broad and ducklike (hence the name "duck-billed" dinosaurs). Webbed feet were characteristic of this type; other species developed great armor plates as protection against the carnivorous saurischians. *Ankylosaurus* (Fig. 227), which has been dubbed "the reptilian tank," had a broad, flat body, covered with an armor plate and with large, laterally projecting spines. Still other ornithischians of the Cretaceous period developed bony plates around the head and neck. One of these, *Triceratops* had two horns over its eyes and another over its nose—all 3 feet long.

At the end of the Cretaceous all the dinosaurs, as well as many other reptiles, became extinct. The causes of this are not known with certainty, but probably the change in climate accompanying the Rocky

Mountain Revolution decreased the plant food available for the herbivores, thus indirectly decreasing the food for the carnivores. Another explanation is that when the swamps dried up at the end of the Cretaceous, the herbivorous dinosaurs were too large to walk about on land. And then, too, many mammals had appeared on the scene which lived by sucking the dinosaur eggs. Probably a combination of these factors provides the reason for the dinosaurs' extinction.

Two other groups of Mesozoic reptiles, separate from each other and from the dinosaurs, were the marine **plesiosaurs** and **ichthyosaurs** (Fig. 226). The former were characterized by an extremely long neck, which took up over half of their total length. The trunk was broad, flat and rather turtlelike, the tail was small, and the animal paddled along by means of finlike arms and legs. Often it was 45 feet long. The ichthyosaurs (fish reptiles) had a body form superficially like that of a fish or a whale, with a short neck, a large dorsal fin, and a sharklike tail. They swam by wiggling their tails using their feet only for steering. It is believed that the ichthyosaur young were born alive, after having hatched from eggs within the mother, for the adults were too specialized to come out on land, and a reptile egg will drown in water. The presence of skeletons of the young within the body cavity of adult fossils has strengthened this theory.

Other Mesozoic Evolutionary Trends. Although the reptiles were the dominant animals of the Mesozoic, many other important organisms evolved during that time: snails and bivalves increased in number and kind; sea urchins reached their peak; mammals originated in the Triassic; and teleost fishes and birds arose during the Jurassic. Most of the modern orders of insects appeared early in the Mesozoic. As for the plants, during the early Triassic, the most abundant types were seed ferns, cycads and conifers; but by the Cretaceous, many others, resembling present-day species, had appeared—sycamores, magnolias, palms, maples and oaks.

From the Jurassic, excellent fossils have been preserved, showing even the outlines of feathers, of the earliest species of bird. This creature, called *Archeopteryx*, was about the size of a crow, had rather feeble wings, jawbones armed with teeth, and a long, reptilian tail, covered with feathers (Fig. 228). Fossils have been found in Cretaceous rocks of two other bird species—*Hesperornis*, an aquatic diving bird that had lost the ability to fly, and *Ichthyornis*, a powerful flying bird, about the size of a pigeon, with reptilian teeth. Modern toothless birds evolved early in the following era.

5. The Cenozoic Era (The Age of Mammals). With equal justice, the Cenozoic could be called the Age of Birds, the Age of Insects or the Age of Flowering Plants, for it is marked by the evolution of all these forms as much as by the evolution of the mammals. It extends from the Rocky Mountain Revolution, some 65,000,000 years ago, to the present, and is subdivided into two periods, the **Tertiary**, which lasted some 64,000,000 years, and the **Quaternary**, which includes the last million, or million and a half, years.

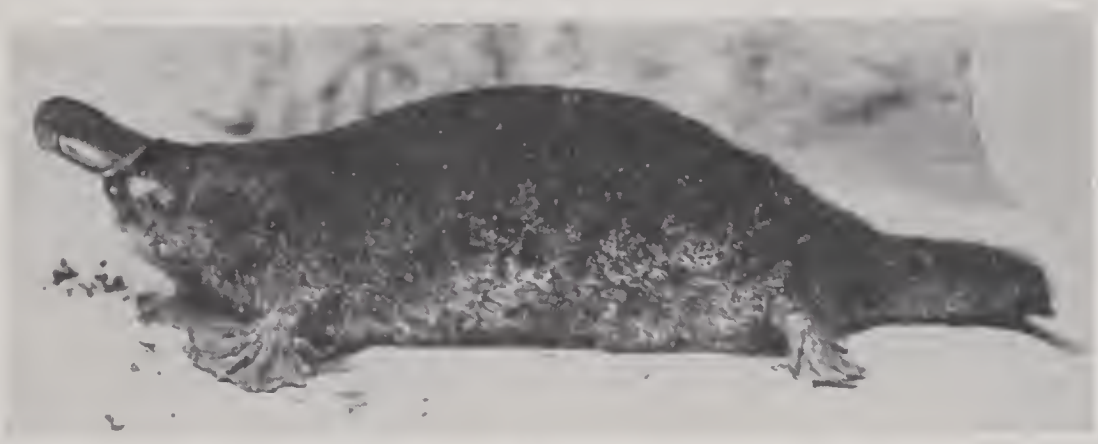
The Tertiary Period. The Tertiary is subdivided into five epochs.

named, from earliest to latest, **Paleocene, Eocene, Oligocene, Miocene** and **Pliocene.** Since the rocks of all these epochs are much the same, the epochs are differentiated chiefly on the basis of the kinds of fossils in the strata. The Rockies, formed at the beginning of the Tertiary, were con-

Fig. 228. Restoration of two of the earliest birds, of the genus *Archeopteryx.* (After Heilmann; Lull, R. S.: Organic Evolution, The Macmillan Co.)

siderably eroded by the time of the Oligocene, giving the North American continent a gently rolling topography. In the Miocene another series of uplifts raised the Sierra Nevadas and a new set of Rockies, and resulted in the formation of the western deserts. The climate was milder in the Oligocene than it is at present, and palms grew as far north as

Wyoming. The uplift begun in the Miocene continued in the Pliocene and, coupled with the ice ages of the Pleistocene, killed many of the mammals and other forms that had evolved. The final elevation of the Colorado Plateau, which also caused the cutting of Grand Canyon, occurred almost entirely in the short Pleistocene and Recent epochs.



A

B

Fig. 229. Two living examples of monotremes—mammals that lay eggs. *A*, The duck-billed platypus. Note the short fur, webbed feet, horny, duck-shaped beak and unusual tail. *B*, The spiny anteater, about 18 inches long, is covered with strong, pointed spines, yellow with black tips. Its narrow black snout is cylindrical, and it captures its food (mostly ants) with the long, protrusible tongue, which is covered with sticky saliva. (Photographs, courtesy of the Australian News and Information Bureau.)

The earliest fossils of true mammals were deposited late in the Triassic, but by the Jurassic there were four orders of mammals, all about the size of a rat or small dog. These earliest mammals **(monotremes)** were egg-laying animals, and their only living survivors are the duck-billed platypus and the spiny anteater (Fig. 229) of Australia. Both have fur and suckle their young, but like turtles they lay eggs. The

Fig. 230. Kangaroo mother with her young in her pouch. (Photograph, courtesy of the Australian News and Information Bureau.)

Fig. 231. Restoration of an archaic meat-eating mammal, a creodont from the Eocene Period, eating a tiny ancestral horse, *Eohippus*. (Copyright, American Museum of Natural History, New York.)

Fig. 232. Restoration of a scene at the Rancho La Brea tar pits (now a part of Los Angeles, California) in the Pleistocene. Many well-preserved specimens of animals now extinct have been found imbedded in the asphalt. In the left foreground are two saber-toothed tigers; in the right foreground, three large ground sloths; the giant vultures, now extinct, had a wingspread of 9 feet. In the background are mastodons and dire wolves. (Copyright, American Museum of Natural History, New York, from a painting by Charles R. Knight.)

ancestral, egg-laying mammals certainly must have differed from the specialized platypus and anteater, but the fossil records of those early forms are incomplete. The present-day monotremes have been able to survive this long only because they lived in Australia, which, until recently, had no placental mammals to offer competition.

By the Jurassic and Cretaceous most mammals were advanced enough to bring forth their young alive, although the most primitive of them—the **marsupials**—gave birth to underdeveloped young which had to remain for several months in a pouch of the mother's abdomen, containing the nipples. The Australian marsupials, freed, like the monotremes, of competition from better-adapted placental mammals, which were responsible for the extinction of their cousins on other continents, evolved into a wide variety of types that superficially resemble some of the placentals; there are marsupial mice, shrews, cats, moles, bears, and one species of wolf, as well as a number of forms with no placental counterparts, such as the kangaroo, wombat and wallaby (Fig. 230). During the Pleistocene there were giant kangaroos in Australia, and wombats the size of a rhinoceros. The opossum more closely resembles the primitive, ancestral marsupial type than do any of these more specialized forms; oddly, it is the only marsupial found outside Australia and South America.

The advanced, modern placental mammals, including man, which are distinctive in bringing forth their young alive and ready to live an independent existence,* evolved from an insect-eating, tree-dwelling ancestor; fossils of this animal in Cretaceous rocks show it to have been tiny and rather like the present-day shrew. Some of these ancestral mammals remained in the trees and gave rise, through a series of intermediate forms, to the primates—monkeys, apes and men; others lived on or under the ground and, during the Paleocene, evolved into a variety of forms—that is, into all the other mammals living today. The archaic mammals of the Paleocene had conical, reptilian teeth, five digits on each foot, and a small brain; they also walked on the soles of their feet instead of on their toes. During the Tertiary the evolution of grasses which served as food, and forests which afforded protection was an important factor in changing the mammalian body pattern. Concomitant with a tendency toward increased size, the mammals all displayed tendencies toward an increase in the relative size of the brain, and toward changes in the teeth and feet. As modern forms, better equipped for survival arose, the archaic mammals became extinct.

Although fossils of both marsupial and placental animals have been found in Cretaceous rocks, it is rather surprising to find the remains of highly developed mammals in strata of the early Tertiary. Whether they actually arose at that time or had existed before in the highlands, and had not been preserved, is unknown.

In the Paleocene and Eocene epochs the first carnivores, called **creodonts** (Fig. 231), arose from the primitive insect-eating placentals.

* That they can do this is due to the placental connection between the fetus and the uterine wall which enables the young to be nourished inside the mother's body for a comparatively long time.

They were replaced in the Eocene and Oligocene by more modern forms which eventually gave rise to the present-day carnivores, such as cats, dogs, bears and weasels, as well as to the web-footed, marine carnivores —the seals and walruses. One of the most famous fossil carnivores is the saber-toothed tiger (Fig. 232), which became extinct only recently in the Pleistocene. These animals had tremendously elongated, knifelike upper canine teeth, and a lower jaw that could be swung down and out of the way, allowing the teeth to be used as sabers for stabbing the prey.

The larger herbivorous mammals, most of which have hooves, are sometimes referred to as the **ungulates.** They do not form a single, natural group, but consist of several independent lines, so that, although both horses and cows have hooves, they are no more closely related than either one is to a tiger. The molar teeth of ungulates are flattened and enlarged to facilitate the chewing of leaves and grass. Their legs have become elongated, and adapted for the rapid movement necessary to escape predators. The earliest ungulates, called **condylarths,** appeared in the Paleocene; they had long bodies and tails, flat, grinding molars, and short legs ending in five toes, each of which bore a hoof. Corresponding to the archaic carnivores, or creodonts, were the archaic ungulates called **uintatheres.** During the Paleocene and Eocene some of these were as large as elephants, and some had three large horns projecting from the top of the head.

The fossil record of several ungulate lines—the horse, the camel and the elephant—are complete, and it is possible to trace the evolution of these animals from small, primitive, five-toed creatures. The chief evolutionary tendencies in the ungulates have been toward an increase in the over-all size of the body and a decrease in the number of toes. The ungulates were early divided into two groups, one characterized by an even number of toes, and including the cow, sheep, camel, deer, giraffe, pig and hippopotamus; the other characterized by an odd number of toes, and including the horse, zebra, tapir and rhinoceros. The elephants and their recently extinct relatives, the mammoths and mastodons, can be traced back to an Eocene ancestor the size of a hog which had no trunk. This primitive form, called *Moeritherium*, was close to the stem that also gave rise to such dissimilar creatures as the coney (a small, woodchuck-like animal found in Africa and Asia) and the sea cow.

The whales and porpoises descended from whalelike forms of the Eocene, called **zeuglodonts,** which in turn are believed to have evolved from the creodonts. The evolutionary history of the bats can be traced to ancestral, winged types, also of the Eocene, which descended from the primitive insectivores. The evolutionary history of some of the other mammals—the rodents, rabbits and edentates (anteaters, sloths and armadillos)—is less well known.

The Quaternary Period (The Age of Man). The Quaternary period, which includes the final million or million and a half years of the earth's history, is usually divided into two epochs, the **Pleistocene,** and the **Recent,** which began some 25,000 years ago with the recession of the

last iee sheet. The Pleistoeene was marked by four periods of glaeiation, between whieh the sheets of iee retreated. At their greatest extent these ice sheets eovered nearly 4,000,000 square miles of North America, extending south as far as the Ohio and Missouri rivers. The Great Lakes, whieh were carved out by the advaneing glaeiers, ehanged their outlines radieally a number of times, and from time to time they emptied into the Mississippi. It is estimated that in the past, when the Mississippi drained lakes as far west as Duluth and as far east as Buffalo, its volume was more than sixty times as great as at present. During the Pleistocene glaciations enough water was removed from the sea and loeked in the iee to lower the sea level 200 to 300 feet; therefore land eonneetions existed that have disappeared since—between Siberia and Alaska at Bering Strait, and between England and the continent of Europe.

The plants and animals of the Pleistoeene were similar to those alive today. It is sometimes difficult to distinguish between Pleistocene and Plioeene deposits, beeause the organisms were similar and nearly modern in form. A eonsiderable number of mammals, including the sabertoothed tiger, mammoth and giant ground sloth, became extinct during the Pleistoeene, after the appearance of primitive man. As for the plant kingdom, the Pleistoeene was marked by the extinction of many species espeeially woody ones, and the appearance of numerous herbaeeous forms.

Paleontology thus tells a story of incessant alteration—of animals struggling with each other for the neeessities of life, of the survival of the fittest and the extermination of the less competent. The fossils which have been found make it impossible to doubt that speeies different from the present ones did exist, and from them we can fill in the gaps between the modern day speeies, and trace baek, step by step, the development of many animals to their primitive ancestral stoek. In short, paleontology tells us in unmistakable, pictorial form a great part of the evolutionary story.

QUESTIONS

1. List the various kinds of paleontological evidence. Why are fossils difficult to find?
2. Name some of the forms of life of the Proterozoic.
3. What were the most common animals of the Cambrian period?
4. Explain how estimates of geologic time are made on the basis of radioactive elements.
5. In what period did vertebrates first appear?
6. What were the two great events of the Silurian period?
7. When was the Age of Fish?
8. What is the significance of the name "Carboniferous?"
9. What was the Appalachian Revolution? When did it occur and what were its effects?
10. What is meant by the term "stem" reptile? What relation do turtles bear to these animals?
11. What factors are believed to have caused the extinction of the dinosaurs?
12. When did the mammals originate?
13. What is the significance of *Archeopteryx?*
14. What are monotremes? What are marsupials?
15. What were the creodonts?
16. Briefly trace the evolution of the various phyla from the beginning to the present. Do you see any signs of teleology?

SUPPLEMENTARY READINGS

Lull, R. S.: *Organic Evolution.* 2d ed. New York, The Macmillan Company, 1935.
A classic reference book that is interesting and readable.

Raymond, P. E.: *Prehistoric Life.* Cambridge, Harvard University Press, 1939.
An interesting account of paleontology.

Schuchert, C., and Dunbar, C.: *Textbook of Geology.* New York, John Wiley & Sons, Inc., 1941,, Part II, Historical Geology.
A detailed presentation of the geological eras and periods.

CHAPTER 28

THE LIVING EVIDENCE FOR EVOLUTION

THE PALEONTOLOGICAL facts comprise only one of two main types of evidence for evolution. In this chapter, the anatomy, physiology and biochemistry of modern plants and animals, their embryologic and genetic histories, and the manner in which they are distributed over the earth's surface, will be considered.

1. The Anatomic Evidence. In the chapters on the plant and animal kingdoms we found that living organisms are classified on the basis of structural similarities and differences. We found, too, that not all similarities afford a basis for classification, but only the similarities of homologous organs. Such organs, you will recall, have not only a similar construction, but also a similar relationship to adjacent organs, and a similar embryonic origin, although they may perform quite different functions. Thus, a seal's front flipper, a bat's wing, a cat's paw and a human hand, though superficially dissimilar, and adapted for the quite different functions of swimming, flying, walking and grasping, respectively, are fundamentally alike, for each consists of almost exactly the same number of bones, muscles, nerves and blood vessels, arranged in exactly the same pattern. Moreover, these organs all have similar embryologic origins. Another illustration of homology is provided by the seven neck vertebras that all mammals have except the sea cow (which seems to have lost one along the way). In the whale, which has no neck, properly speaking, the vertebras are no more than flattened disks, and in the giraffe they may be 12 to 20 inches long; but always the number is the same.

The science of taxonomy was established on such grounds as these long before the fact of evolution was known, but by and large, its classifications have stood the test of time and are supported today by other types of evidence. The classification of modern-day organisms into well-defined groups—phyla, classes, orders, species and so on—is possible only because most of the intermediate forms have become extinct. If every animal and plant that ever lived were still living today, it would be a difficult matter to divide the living world into neat taxonomic categories, for there would be a continuous series of forms grading from lowest to highest. The species now living have been called "islands in a sea of death," and have been likened also to the terminal twigs of a tree of which the trunk and main branches have disappeared. The problem of the taxonomist is to reconstruct the missing branches and put each twig on the proper branch.

Vestigial Organs. A second type of anatomic evidence for evolution is provided by the fact that in almost every species of plant and animal

are organs or parts of organs which are useless and degenerate, often undersized or lacking some essential part, as compared to homologous structures in related organisms. In the human body there are more than 100 such **vestigial organs,** including the appendix, the coccyx (the fused tail vertebras), the wisdom teeth, the nictitating membrane of the eye, the body hair, and the muscles that move the ears. Comparative anatomy indicates that such organs are the remnants of ones which were functional in some earlier animal. Because of a change in the environment or mode of life of the species, the organ became unnecessary for survival and, gradually, nonfunctional. Mutations are constantly occurring which decrease the size and function of various organs, of course, and if the organs are necessary for survival, the organisms undergoing such mutations will be eliminated. The structures we recognize as vestigial organs are simply in the process of being eliminated.

The human appendix is the remnant of a blind pouch, the **cecum,** which is a large, functional structure in the digestive tract of herbivorous animals like the rabbit. Foods rich in cellulose require a long time for digestion, and the cecum provides a place where the food may be stored while the gradual process of digestion, mostly by intestinal bacteria, takes place. A long time ago in our evolutionary history, our ancestors changed to a diet containing more meat and less cellulose, and the cecum has gradually diminished to the present useless vestige, the appendix.

The nictitating membrane—the small flap of tissue in the inner corner of the eye—is another human vestigial organ which can still be observed fully developed and functional in such animals as reptiles, cats and birds. In man it is the remains of a transparent third eyelid which was capable of covering the entire eye from the inner to the outer margin. Its purpose was to protect the eye, while allowing the animal to see.

Man is not alone in having vestigial organs: both whales and pythons, for example, have bones imbedded in the flesh of the abdomen which are vestigial hind legs; the wingless birds have vestigial wing bones; many blind, burrowing or cave-dwelling animals have vestigial eyes; and so on.

2. The Evidence from Comparative Physiology and Biochemistry. Perhaps no evidence could be more convincing of the relationship between plants and animals of related species than the similarity to our own bodies displayed by any of the mammals. It is startling to find, upon dissecting a rat for the first time, a replica of the human heart, lungs, stomach and most of the other organs, and to realize that these structures are functioning in a manner almost identical to our own. There are, of course, differences—in the vitamin requirements, in the arrangement of a few blood vessels, and in the workings of the reproductive system—but, in general, the important physiological processes of respiration, digestion, circulation, excretion, and nervous response are the same as ours. Yet rats and human beings belong to different orders of the class Mammalia, and frogs, whose internal workings also resemble ours remarkably, belong to a different class!

Blood chemistry has been a particularly fruitful field in yielding evidence of relationships. The degree of similarity between the proteins in the blood of various animals is tested by the antigen-antibody tech-

niques discussed previously (p. 139). An experimental animal, usually a rabbit, is given repeated injections of human blood or serum, containing proteins foreign to the rabbit's blood. In response, the white cells of the rabbit produce antibodies specific for human, blood-protein antigens. The antibodies are then obtained by withdrawing blood from the rabbit and allowing it to clot (the antibodies are in the serum). Even a dilute sample of the serum, when mixed with human blood, results in a visible precipitation caused by the combination of antigens and antibodies. But nonhuman blood, in order to form such a precipitation, requires that the serum be much more concentrated, and even then the precipitation may be delayed or scanty. The blood of quite different animals may cause no precipitation at all. By using a series of rabbits, each injected with the blood of different species, it has been possible to obtain a series of antibodies, each specific for the blood proteins of a particular species of animal.

Thousands of tests involving different animals have revealed a basic similarity between the blood proteins of all the mammals, the degree of relationship being indicated by how much the antigen and antibody solutions can be diluted and still result in visible precipitation. Man's closest "blood relations," as determined in this way, are the great apes; the next closest, in order, are the Old World monkeys, the New World prehensile-tailed monkeys and the tarsioids. Of all the types of primate blood, the lemur's results in the least precipitation when combined with antibodies specific for human blood. As for other animals, the blood protein tests have shown that cats, dogs and bears are more closely related to each other in this regard than to the other mammals, while cows, sheep, goats, deer and antelopes form another closely related group. Seals and sea lions are closer to the carnivores than to the other mammals.

Another interesting discovery stemming from these tests is that there is a closer relationship among the modern birds than there is among the mammals, for all the several hundred species of birds tested so far give strong and immediate reactions with serum containing antibodies for chicken blood. The tests also indicate that birds are more closely related to the turtle-crocodile line of reptiles than to the snake-lizard line, which corroborates the paleontological evidence. Similar differences in the proteins of the body cells can be detected by appropriate techniques.

Still another bit of evidence of relationship between living organisms is provided by the fact that animals and plants differ in their susceptibility to certain diseases, related species, generally speaking, being vulnerable to the same ones (see the discussion of immunity, p. 402). This, like the evidence of the blood tests, is based on fundamental chemical similarities.

Since the kind of wastes excreted depends upon a series of enzymes which act on a corresponding series of chemicals, and since the enzymes are determined by genes which have been selected by evolution, an analysis of the urinary wastes of different species provides evidence of evolutionary relationships. Man excretes certain wastes as uric acid because he has lost in evolution the genes for the enzymes necessary to

convert this to allantoin, urea or ammonia, as do lower animals. This loss has also made him susceptible to gout, a disease caused by the accumulation of uric acid crystals in the joints and muscles.

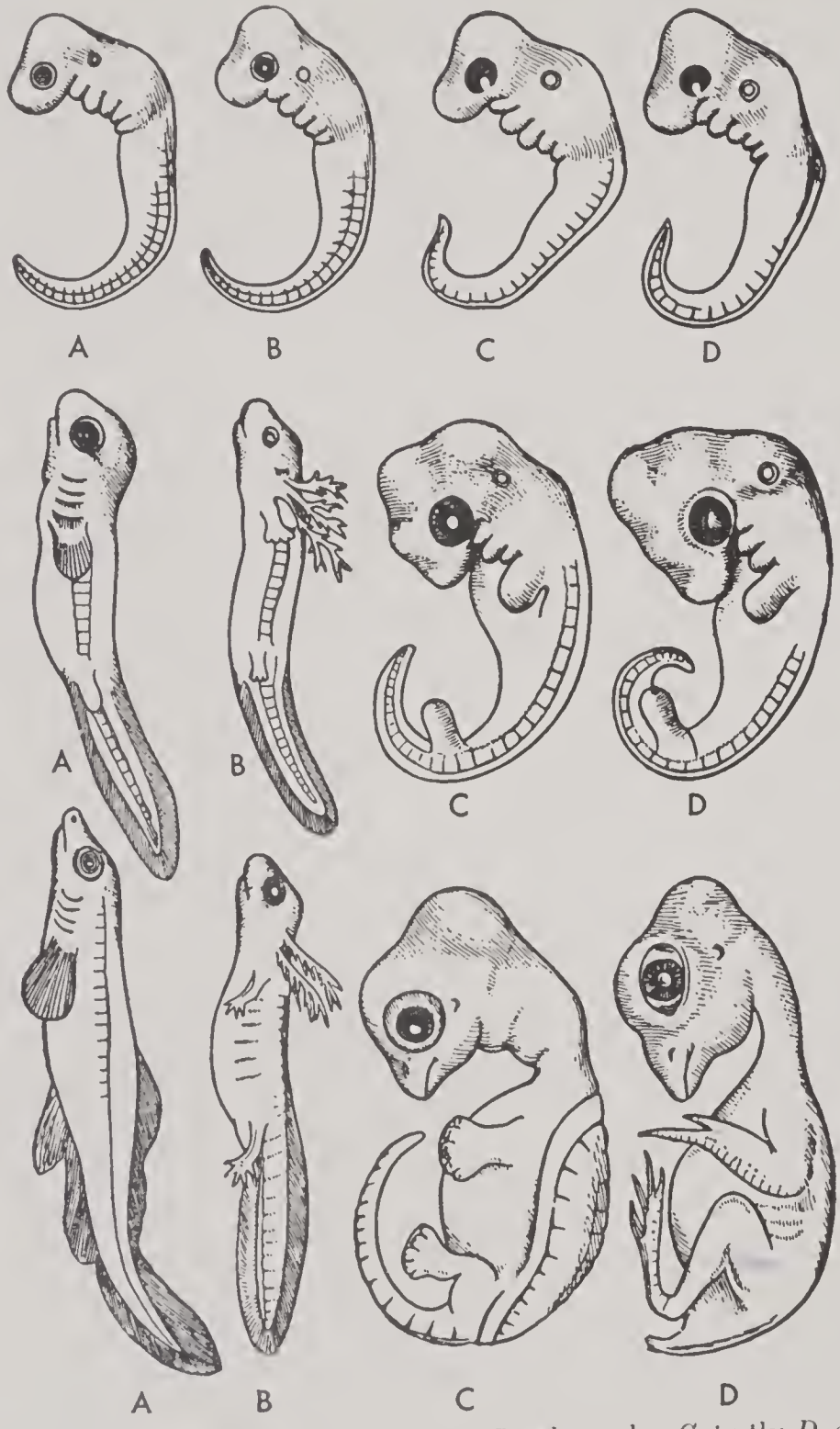


Fig. 233. Embryos of lower vertebrates: *A*, fish; *B*, salamander; *C*, turtle; *D*, chick. Note that the earliest stages of development (top row) are remarkably similar, but that differences become more marked as development proceeds (middle and bottom rows).

3. The Embryologic Evidence. The embryologic evidence of the relationship between animals is even more striking than the anatomic evidence of the adult forms. In fact, during their first stages of growth, vertebrate embryos (Fig. 233, 233a) are so nearly identical that it is difficult to differentiate that of a fish, frog, chick, pig or human from a

mixed group. The reason for this is clear: the early embryonic stages of all of them are relatively simple, because the phenotypic effects of most genes are not manifested until later in development.

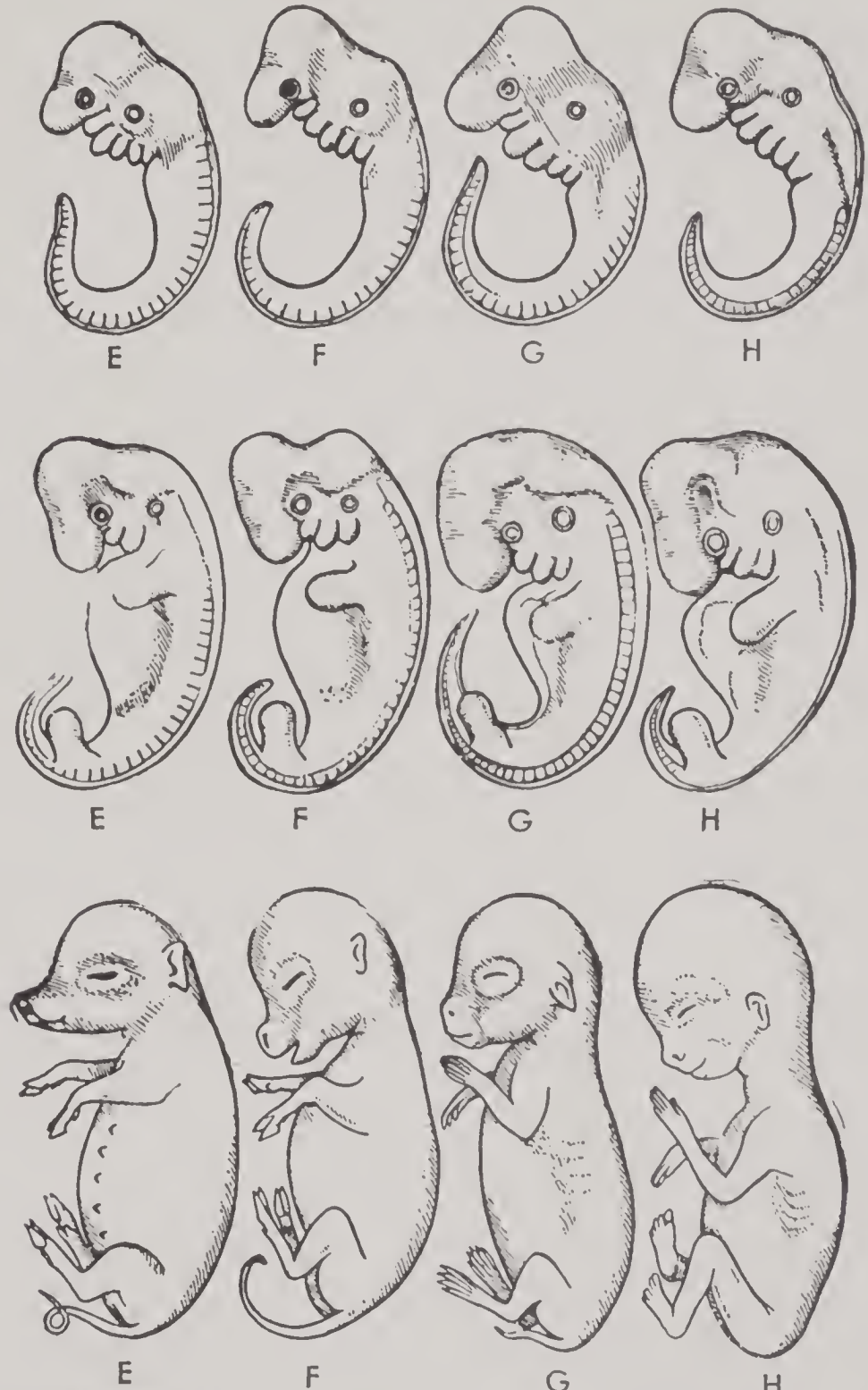


Fig. 233a. Mammalian embryos: *E*, pig; *F*, calf; *G*, rabbit; *H*, human. Note that the earliest stages of these embryos are similar to those of the lower vertebrates and that even the later stages have many common characters. (Lindsay: Evolution and Genetics. After Romanes; Darwin and After Darwin, by permission of the Open Court Publishing Company.)

Because many lower adult animals closely resemble their embryonic forms, it was mistakenly believed for a long time that during development the higher forms recapitulated or repeated the adult forms of lower animals—that is, the members of each species were believed to repeat the stages by which the species has evolved to its present con-

dition. The German biologist Haeckel expressed this idea in 1866 as the **theory of recapitulation.** The concept was extremely important in stimulating research in embryology in a wide variety of species and in emphasizing the general resemblance between embryonic development and the evolutionary process, but it is now known that the embryos of higher forms resemble the *embryos,* not the adults, of lower forms. Obviously, in recapitulating its evolutionary history in a few days, weeks or months, an embryo must skip some steps and distort others; and then, too, later in development the embryos of some of the higher animals exhibit structures not present in their ancestral counterparts, which enable them to develop in a new type of environment. Thus mammalian embryos, although they have many early characteristics in common with those of fish, frogs and reptiles, give rise to additional structures which allow them to survive and develop within the uterus of the mother rather than in an egg shell. These newer, secondary traits frequently modify the original characteristics common to both high and low forms, so that the resemblances are blurred. The concept of recapitulation cannot be applied rigorously to development, but, as modified, it does explain many otherwise inexplicable events.

It is believed, with what appear to be good reasons, that the original, single-celled fertilized egg, which is the beginning of development for all animals, resembles the protozoan ancestor common to them all. This, of course, can be no more than a reasonable guess, since no one knows the nature of that first bit of living stuff.

It is known with certainty, however, that in the second, blastula stage, the developing egg of all animals* resembles such colonial protozoa as *Volvox.* And in the third, gastrula stage, it can be compared to the basic structural plan of the coelenterates, having two layers of cells, with a hollow cavity connected to the outside by a single opening.

After the gastrulation stage, development follows one of two main lines; in one (the echinoderms and chordates) the blastopore—the opening from the gastrular cavity—becomes the anus, or comes to lie near the anus; in the other (the annelids, molluscs, arthropods and others) the blastopore becomes the mouth, or comes to lie near the mouth.

In both lines, a third layer of cells—the mesoderm— develops between the ectoderm and entoderm. In the chordate-echinoderm line this develops, at least in part, as pouches or evaginations from the primitive digestive tract, while in the annelid line the mesoderm originates from special cells differentiated early in development.

Shortly after the appearance of the mesoderm all chordate embryos develop a dorsal, hollow nerve cord, as well as a notochord—the internal supporting rod for the body—and perforations in the pharynx (the gill slits). Thus the early human embryo resembles a fish embryo, with gill slits, pairs of aortic arches, or blood vessels traversing the gill bars, a fishlike heart with a single auricle and ventricle, a primitive pronephros or fish kidney, and a tail, complete with muscles for wagging it. Later the human embryo resembles a reptilian embryo: its gill slits close; the bones which make up each vertebra and which had been separate, as in

* All, that is, which ever progress to the multiple-cell stage.

fish embryos, fuse; a new kidney—the mesonephros—forms, and the pronephros disappears; and the auricle becomes divided into right and left chambers. Still later the human embryo develops a mammalian, four-chambered heart, and a third, completely new kidney, while the notochord regresses, and so on. During the seventh month of intrauterine development the human embryo resembles—in being completely covered with hair and in the relative size of body and limbs—a baby ape more than it does an adult human.

The genetic reason for the phenomenon of recapitulation is as follows. All chordates have in common a certain number of genes which regulate the early developmental processes. But as our ancestors evolved from fish, through amphibian and reptilian phases, they accumulated, by mutations, many new characteristics, though some of the genes for the original fish form were retained. The latter group of genes still control early development. Then, a little later, the genes which the human being still shares with amphibians influence the course of development, so that the animal resembles a frog. This process is repeated when the "reptilian" genes come into control still later. Only after all these stages are passed do the peculiarly mammalian genes assert their influence, and the special primate characteristics are still later in appearing. The anthropoid apes, which have the most immediate ancestors in common with us, naturally have the most genes in common with us too, and therefore their development is almost identical with ours except for the final details. A pig or rat, whose ancestors are the same as ours only up to the primitive, placental mammal or insectivore stage, has fewer genes in common with us, and hence developmental processes that diverge at an earlier time. All this is only to say that, in general, the earliest characters to appear in development are those distinguishing phyla; then those distinguishing classes, orders, families and genera, and, at the very last, the characteristics which distinguish species.

4. The Genetic Evidence. The selection and breeding of domesticated animals and cultivated plants for the past several thousand years provide us with models of how some of the evolutionary forces operate. All the varieties of present-day dogs are descended from one or a few related species of wild dog or wolf, and yet they vary tremendously in many characteristics. Compare, for example, the size of the chihuahua and the St. Bernard or Great Dane; the head shape of the bulldog and collie; the body proportions of the cocker, dachshund and Russian wolfhound. If these varieties were found in the wild, they would undoubtedly be assigned to different species, and perhaps even to different genera. But since all are known to come from common ancestors, and since all are interfertile, they are regarded as varieties or races of a single species.

The plant breeders who developed the present varieties of cultivated plants have similarly produced, by selection and interbreeding, a tremendous variety of plants from one or a few forms. The cliff cabbage, for example, which still grows wild in Europe, is the ancestor, not only of our cultivated cabbage, but of such dissimilar plants as cauliflower, kohlrabi, Brussels sprouts, broccoli and kale. Many varieties of wheat, too, have been produced by selection, each adapted for certain growing conditions. Thus there are winter wheats, spring wheats, wheats re-

sistant to drought, to rusts, and so on. The cultivated species of tobacco has been traced back to a cross between two species of wild tobacco; corn has been traced to teosinte (a grasslike plant growing wild in the Andes and Mexico), and so on. Breeding experiments and observations indicate that species are not, as Linnaeus believed, unchangeable biological entities, each of which was created separately, but groups of organisms which have arisen from other species and which can give rise to still others.

Another type of genetic evidence is provided by microscopic cytological studies of a variety of plants and animals—fruit flies, jimson weeds, primroses, and so on. These investigations, by showing the number of chromosomes and certain details of their structure and arrangement, indicate as clearly as do breeding experiments that living things are related and have evolved from earlier forms.

5. Evidence from the Geographic Distribution of Organisms. Not all plants and animals are found in all parts of the world; they are not even found everywhere that they could survive, as one would expect if climate and topography were the only factors determining distribution. Central Africa, for example, has elephants, gorillas, chimpanzees, lions and antelopes, while Brazil, with a similar climate and other environmental conditions, has none of these, but does have prehensile-tailed monkeys, sloths and tapirs. The present distribution of organisms is understandable only on the basis of the evolutionary history of each species.

The *range* of a given species—that is, the portion of the earth in which it is found—may be only a few square miles or, as with man, almost the entire world. In general, closely related species do not have identical ranges, nor are their ranges far apart; they are usually adjacent, but separated by a barrier of some sort, such as a mountain or a desert.

As one would expect, regions which have been separated from the rest of the world for a long time (such as Australia and New Zealand) have a flora and fauna peculiar to them. Australia has a mammalian population of monotremes and marsupials found nowhere else. This is because, during the Mesozoic, Australia was isolated from the rest of the world, so that its primitive mammals never had any competition from the better-adapted placental mammals which eliminated the monotremes and most of the marsupials everywhere else. Free from this dangerous threat, the primitive mammals could give rise to a variety of forms which were able to take advantage of the different habitats available.

The situation of the oceanic islands is similar to that of Australia and New Zealand, except that these islands arose independently in the middle of the ocean and never have been attached to any continent. Because of their isolation, their floras and faunas are peculiar, made up to some extent of species found nowhere else. The plants and animals of the Galapagos Islands, studied by Darwin during the voyage of the *Beagle,* are similar to those on the nearest mainland—the coast of Ecuador, some 500 miles away, whence their ancestors had flown, swum or been transported. There are no frogs or toads on the Galapagos, even though there are woodland spots ideally suited for such creatures, because neither the animals nor their eggs can survive being exposed to

sea water, an inevitable experience for any animal migrating to the islands. There are no terrestrial mammals, either, although there are many bats, as well as land and sea birds. A number of species of giant lizards and giant turtles also inhabit the island, some living on but a single island of the archipelago. The occurrence of these particular forms—closely related to, yet not identical with, those of the Ecuador coast—suggests strongly that after the first animals and plants arrived on the islands, mutations took place which changed the species slightly, and that these changes were retained because of isolation. It is almost impossible to doubt that these forms offer a good example of one phase of the evolutionary process.

Consider another type of distribution evidence. In all the world, alligators are found only in the rivers of the southeastern United States, and in the Yangtse River of China, and sassafras, tulip trees and magnolias grow only in the eastern United States, Japan and eastern China. There seems to be no logical reason for this situation, except the one provided by the facts of geology. It is known that early in the Cenozoic the northern hemisphere was much flatter than it is now and the North American continent was connected with eastern Asia by a land bridge at Bering Strait, and possibly with Greenland. The climate of this region was much warmer than at present, and fossil evidence shows that alligators, magnolia trees and sassafras were distributed over the entire region. Later in the Cenozoic, as the Rockies increased in height, the western part of North America became colder and dry, causing the plants adapted to a warm, humid climate to become extinct. Then, with the Pleistocene glaciations, the ice sheets moving from the north met the desert and mountain regions in western North America, eliminating any surviving temperate plants; and in Europe the polar glaciations nearly met the glacier spreading from the Alps, so that many of the temperate plants there became extinct. But in the southeastern United States and eastern China there were regions untouched by the glaciation, in which the magnolia trees and alligators survived. Because the alligators and magnolia trees of the two regions have been separated for a million or more years, they have followed separate evolutionary pathways, and so are slightly different, but they are still closely related species of the same genera.

The facts about the distribution of plants and animals constitute the science of **biogeography,** one of the basic tenets of which is that each species of animal and plant originated only once. The particular place where this occurred is known as its **center of origin.** From its headquarters each species spreads out until halted by a barrier of some kind—physical, such as an ocean or mountain, environmental, such as an unfavorable climate, or biological, such as the absence of food or the presence of enemy organisms which prey upon it or compete with it for food or shelter.

The Biogeographic Regions. By studying flora and fauna all over the world, biogeographers have discovered basic patterns of distribution, according to which they have divided the land area into six regions. Although the divisions were originally based on mammalian distribution, they have since been found valid for many other classes of plants and

animals. Note in the following discussion that the areas of any one division are often widely separated, with great variations of climate and topography. The one and only characteristic common to them all is accessibility, at some time in the past, to all the species inhabiting them.

The **Palearctic** region comprises Europe, Africa north of the Sahara Desert, and Asia north of the Himalaya and Nan-Ling mountains, plus Japan, Iceland, the Azores and the Cape Verdes Islands. Some of the indigenous animals are moles, deer, oxen, antelopes, sheep, goats, pheasants, robins and magpies. A few species of some of these forms are also found in the Nearctic region.

The **Nearctic** region includes only Greenland and North America as far south as the northern plateau of Mexico. Besides many of the same forms characteristic of the Palearctic, it supports species of opossums, skunks, raccoons, blue-jays and turkey buzzards found nowhere else. The land bridge connecting North America and Asia at Bering Strait in former geologic times was used by many migrating animals and plants; hence the similarity of the fauna and flora of the Palearctic and Nearctic regions. Because the two regions have such similar forms, they are often referred to in combination as the **Holarctic** region.

The **Neotropical** region consists of South America, Central America, southern Mexico and the islands of West Indies. It has a distinctive fauna, including alpacas, llamas, prehensile-tailed monkeys, bloodsucking bats, sloths, tapirs, anteaters and a host of bird species found nowhere else in the world.

The part of Africa south of the Sahara, plus the island of Madagascar, makes up the **Ethiopian** region. The gorilla, chimpanzee, zebra, rhinoceros, hippopotamus, giraffe, aard-vark and many birds, reptiles and fishes live only in this region.

The **Oriental** region includes India, Ceylon, Indo-China, southern China, the Malay peninsula and some of the islands of the East Indies. Outstanding of the animals peculiar to it are the orang-utan, black panther, Indian elephant and gibbon.

The sixth and last region, called the **Australian,** includes Australia, New Zealand, New Guinea and other islands of the East Indies. The imaginary dividing line between the Oriental and Australian regions, known as **Wallace's Line,** separates Bali and Lombok, goes through the straits of Macassar between Borneo and Celebes, and then passes east of the Philippines. Although the islands of Bali and Lombok are separated only by a channel 20 miles wide, their respective animals and plants are more unlike than are those of England and Japan—almost half a world apart. Native to the Australian region are the duck-billed platypus, kangaroo, wombat, koala bear and other marsupials. And among its strange assortment of birds are the emu and cassowary (both flightless birds), the lyre-bird and cockatoo.

Every aspect of the present living scene contributes its own clues to the puzzle of "how things got this way." The point is sometimes raised that of the foregoing types of evidence, none, by itself, provides proof positive that evolution has occurred. Taken together, however, and added to the evidence provided by paleontology, the facts do not admit

of a reasonable doubt that the present forms of life have evolved from other, quite different ones. And many of the facts of physiology, biochemistry and embryology can be interpreted meaningfully only in the light of the theory of organic evolution.

QUESTIONS

1. Give, briefly, the various types of living evidence for evolution. Which do you think is the strongest?
2. What is the theory of recapitulation? How has it been modified, and what is its great significance in the present form?
3. Discuss the genetic basis of the theory of recapitulation.
4. Explain why the marsupials are widespread in Australia and almost nonexistent elsewhere.
5. How do you explain the fact that the animals and plants of England and Japan are similar, though they are nearly half a world apart?
6. What additional vestigial organs of the human body can you think of?
7. If, in tracing evolutionary relationships, you found that anatomic evidence pointed one way, and biochemical evidence the other, which do you think would be the more reliable? Why?

SUPPLEMENTARY READINGS

Baldwin, E.: *Comparative Biochemistry.* New York, The Macmillan Company, 1938.
An interesting account of biochemical similarities in different animals which point to evolutionary relationships.

Florkin, M.: *Biochemical Evolution.* New York, Academic Press, Inc., 1949.
A detailed but readable discussion of biochemical facts bearing on evolution.

CHAPTER 29

THE EVOLUTION OF MAN

NOW THAT WE have reviewed the highlights of the evolutionary process preceding man's appearance on the scene, we are in a position to understand why man is classed in the phylum Chordata, subphylum Vertebrata and class Mammalia. We have only to pick up the thread of the story where we left it with the emergence of the mammals and follow it through to the present. When we have finished we shall see why man belongs also to the order of mammals called the **Primates**, the family **Hominidae**, the genus *Homo* and the species *sapiens*. To do this, we must begin, not with man's emergence in his present form in the Pliocene or Pleistocene (the exact time of the event is unknown), but with the development of the primates in the Eocene. But, first, let us take a quick glance at all the kinds of primates existing today.

I. MAN AND THE OTHER PRIMATES

The taxonomist Linnaeus used the term "primate," meaning "first," to indicate that this group of animals was of first importance. Although this viewpoint was naive, the name is appropriate, for the primates were probably among the first orders of mammals to become distinct, and they are still much closer than many mammals to the original, primitive, shrewlike ancestor common to them all. This fact is sometimes expressed by saying that the primates are unspecialized, for, in spite of their convenient prehensile limbs, large brains and eyes directed forward, their limbs still end in five digits, and their teeth are unadapted for eating any one particular kind of food.

The most primitive of the primate suborders is made up of the **lemurs** (Fig. 234), which live in the tropics of Africa and Asia and are especially abundant on the island of Madagascar. They are small, tree-living animals, superficially rather like squirrels, with a fairly long muzzle, eyes directed more to the side than forward, and a well-developed tail. Although some of the toes end in claws, the thumbs and big toes are covered by nails and are widely separated from the other digits.

The second suborder of the primates is represented today by a single species of arboreal, nocturnal animal, called *Tarsius*, found in the East Indies. *Tarsius* is about the size of a rat, but has long hind legs and moves by hopping. It is characterized by enormous eyes, directed forward, and a relatively large brain. The muzzle is short, illustrating the beginning of the kind of face common to the higher primates.

The third suborder, **Anthropoidea**, includes all the rest of the primates —monkeys, apes and man. These animals have a larger and more complicated brain than the other primates, eyes directed forward to provide stereoscopic vision, and a spot (the fovea) in the center of the retina where vision is especially acute. Most of the anthropoids normally walk

on all fours, but all of them tend to sit upright, so that the hands are free to handle objects.

The suborder Anthropoidea is subdivided into two groups, the **Platyrrhines,** or broad-nosed monkeys, found in South and Central America, which have widely separated nostrils, directed forward and sideward, giving the nose a broad, flat appearance; and the **Catarrhines,** characterized by a much narrower nose with the nostrils closer together and directed downward.

The platyrrhines represent a group of primates, isolated in South America during the Tertiary, that underwent an evolution independent of the other primates. Living platyrrhines are the marmoset, or squirrel monkey; the capuchin monkey—the organ-grinder's companion; and the spider monkey (Fig. 235). Most of the platyrrhines have a well-developed prehensile tail used as a fifth hand for grasping objects and hanging from trees, and the group is sometimes called the prehensile-tailed monkeys.

The catarrhines include three groups—Old World monkeys, anthropoid apes and man—all of which have the same dental formula, a large brain, toes and fingers with flattened nails, and either a short, nonprehensile tail or none. The group of Old World monkeys is large, including the macaque, guenon (Fig. 236), mandrill, mangabey, baboon, langur, proboscis monkey and many others. All these monkeys tend to sit upright, and all have buttocks with bare, hardened sitting-pads, called **ischial callosities,** which are frequently a brilliant red or blue. The mandrills and baboons have taken to living on the ground instead of in trees, but they walk on all fours, have an elongated snout and large canine teeth. Baboons are intelligent animals which travel in troops and cooperate in obtaining food and protecting the females and young.

The second group of catarrhines—the anthropoid or manlike apes—includes four living types: the gibbon, orang-utan, chimpanzee and gorilla. These apes have rudimentary tails or none at all, arms longer than their legs, a semierect posture, opposable thumbs or great toes, and chests that are broad like man's rather than thin and deep like that of most mammals. Their brains are larger than those of the lower primates and more like man's in the pattern and relative size of the parts. They range in size from the 3 foot gibbon to the gorilla, which is 6 feet tall and weighs as much as 600 pounds.

Gibbons (Fig. 237), found in Malaya, have arms so long that they reach the ground when the animal walks erect. The usual mode of locomotion, called brachiating ("arming"), is by swinging through the trees from limb to limb, which allows the animal to clear as much as 40 feet at a time. The spectacular aerial acrobatics of the gibbon require great agility, coordination, good eyesight and the ability to make rapid judgments of distance and possible landing sites.

The orang-utan (Fig 238) is a native of Borneo and Sumatra. Although heavy and powerful, the animal is scarcely 5 feet tall because of its short legs. An adult male may weigh 160 pounds and have a brain capacity of over 500 cc. (the average human brain capacity is about 1500 cc.). Aided by their enormously long arms, sometimes with a span of 8 feet, orang-utans are successful arboreal animals, but because of

Fig. 234. Ring-tailed lemur, one of the most primitive of living primates. (Courtesy of the San Diego Zoo.)

their great weight they are more deliberate in their movements than the gibbon, and must test the strength of tree branches before springing upon them.

Chimpanzees and gorillas both live in Africa and have many characteristics in common, in addition to those they share with the other anthropoid apes; there is, in fact, a particularly close relationship between them. An adult chimpanzee (Fig. 239) weighs about 110 pounds. and is between 5 and 5½ feet tall. Like the orang-utans, chimpanzees build nests in trees at night and for noonday siestas; but although primarily tree-dwellers, they are quite at home on the ground for their legs are longer and their arms shorter than those of an orang. In recent years, psychologists such as Dr. Robert Yerkes and his associates at the Yale Laboratory of Primate Biology in Winter Park, Florida, have made extensive studies of the mentality and behavior of the great apes, and of chimpanzees in particular. These studies show that apes are strikingly curious, perceptive and "reasonable," with strong emotions and well-developed social instincts. On the basis of present data, the chimpanzee appears to be, of all the apes, the closest to man in intelligence. but Dr. Yerkes believes that if comparable studies were made with gorillas, which have the largest brain of any living ape (600 cc.), they might prove to be even more intelligent than chimpanzees, in spite of the fact that they are less docile, imitative and suggestible.

Gorillas (Fig. 240) are not only the largest of the primates; they are, weight for weight, the strongest—several times stronger than man. The gorilla's legs are relatively short, the arms are more human in their proportions than those of the other apes, and the hands are relatively short and wide—quite like human hands. The massive head has large, bony crests on top of the skull for the attachment of the neck and jaw muscles. Gorillas, too, are ground-dwellers, although they occasionally build sleeping nests in low trees, and have feet adapted for walking rather than for swinging through the trees. Like man, they walk on the soles of the feet with the toes extended, rather than curled under, in the fashion of the other apes. Normally, gorillas walk on all fours,

Fig. 235. Spider monkey, a New-World monkey with a strong prehensile tail, used in swinging from tree to tree. (Courtesy of the San Diego Zoo.)

Fig. 236. Old World monkeys (De Brazza guenons); an adult pair and a six-month old infant. (Courtesy of the San Diego Zoo.)

Fig. 237. An anthropoid, the white-banded gibbon. These apes use their long arms to swing from tree to tree with great agility. (Courtesy of the San Diego Zoo)

Fig. 238. An eight year old male orang-utan. Note the opposable big toe on the handlike foot. (Courtesy of the San Diego Zoo.)

Fig. 239. An adult female chimpanzee and her sixteen month old child. (Courtesy of the San Diego Zoo.)

but, when attacking, they usually rear up on their hind legs. Although they will accept meat, they are ordinarily vegetarians, preferring such foods as bananas, carrots and nuts.

Man, the last of the giant apes, is placed in a different family (Hominidae). Although the gulf may appear to be great between the apes and ourselves, the anatomical differences distinguishing us from

Fig. 240. Mbongo, an adult male mountain gorilla. When this picture was taken, he was thirteen years old and weighed 602 pounds. Gorillas normally assume the four-footed posture illustrated, when walking on the ground. The massive crest on the top of the head, peculiar to the mountain gorilla, is absent from the lowland forms of western Africa. (Courtesy of the San Diego Zoo.)

them are relatively few; almost every bone, muscle, internal organ and blood vessel of the ape is repeated in man. The differences are primarily those of proportion and are correlated with our ground-living way of life. These differences, which justify man's being placed in a separate family, are as follows: (1) Man's brain is larger, being two and a half to three times as large as the gorilla's. (2) The human nose has a prominent bridge and a peculiar, elongated tip. (3) Man's upper lip has

a median furrow, and his lips are rolled outward, revealing the mucous membranes. (4) Man has a jutting chin, and apes have none. (5) Man's great toe is not opposable, but is in line with the others. (6) The human foot is adapted for bearing weight by being arched both lengthwise and crosswise. (7) Man is relatively hairless. (8) Man's canine teeth project little, if at all, beyond the line of the other teeth. (9) Man has an erect posture.

No single ape resembles man in all traits more than do the rest; some are closer in certain respects, some in others. The gorilla, for instance, has hands, feet and a pelvis more like man's than are those of any other ape, but the chimpanzee's skull and skin color are the most like the human being's. The orang-utan is the only ape to have exactly the same number of ribs that we have, and it also has our high forehead, while the gibbon most closely resembles us in the relative length of its legs, in its posture and its gait on the ground. In regard to any structure or proportion, the difference between man, the gorilla and the chimpanzee is not so great as the difference between any of these animals and the monkeys.

II. FOSSIL PRIMATES

The earliest known primate fossils are those of lemuroids and tarsioids, found in Paleocene rocks in both North America and Europe. These animals are believed to have descended from the tree-living insectivores of the late Cretaceous, which resembled present-day tree shrews. Since that time the lemurs have evolved separately and have not given rise to any other forms. The tarsioids, in contrast, gave rise to both New and Old World monkeys, each of which evolved separately from different tarsioids during the Eocene. The New World monkeys have had a separate evolutionary history since the Eocene and represent side branches rather than segments of the main evolutionary trunk leading to man.

The oldest Old World monkey, *Parapithecus,* fossils of which have been found in Lower Oligocene rocks in Egypt, was smaller than any modern monkey or ape, and was near the stem leading to man (it had the same dental formula). This animal probably represents the common ancestor of today's Old World monkeys, anthropoid apes and man. From this point, the evolution of the modern Old World monkeys diverged from that of the higher primates.

The rocks of the Lower Oligocene also contain fossils of the first anthropoid ape, named *Propliopithecus,* which probably descended from *Parapithecus* and was close to the common ancestor of man and all anthropoid apes. This little gibbon-like animal showed the first adaptation toward an upright sitting posture which characterizes the apes as well as gibbons. (In all apes the tail has disappeared, and the muscles which formerly wagged the tail have spread out to cover the floor of the pelvis and help support the abdominal organs.) Another human-like characteristic of *Propliopithecus* was the balanced position of the skull on the end of the vertebral column.

During the Miocene, giant primates evolved from these primitive anthropoids, and by the middle of that epoch the evolutionary lines

leading to the various types of modern anthropoids were distinct. The orang-utans probably differentiated from the common stock earlier than the others, for fossils of the ancestor of the orang-utan, *Paleosimia,* have been found in India in Miocene deposits.

The animal which comes closest to being the common ancestor of the gorilla, chimpanzee and man is *Dryopithecus* (Fig. 241), an anthropoid ape of the Miocene with characteristics found today only in these three groups. Thus the line which eventually gave rise to modern man has been separate from those leading to the present-day apes for about 25,000,000 years. Just when man's ancestors left the trees and took up a terrestial life, and what the stimulus for this move was, are still not known. Although the primate fossil record is relatively scanty, more fossils of this stage in evolution have been found in the past twenty years than ever before, and it is possible that in the future the fossil record will supply answers to these questions.

In recent years, fossils of manlike apes dating from the Pleistocene or late Pliocene have been found in the Transvaal, South Africa. Although the animals which left these remains existed too recently to be man's ancestors, they probably represent a structural stage just preceding that of man, and may indeed be descendants of the immediate human ancestor that survived unchanged from man's Pliocene ancestors.

One of these Pleistocene fossils, found in 1938 and named *Paranthropus,* has a skull shape and profile essentially apelike, but its brain capacity is 650 cc., greater than that of any known ape, and almost as large as that of the earliest fossil ape-man. Its cheekbone, jaw-hinge and teeth are almost identical with man's. And the foramen magnum (the hole in the back of the skull through which the spinal cord emerges) is like man's in being far under the skull, indicating that the animal walked more nearly erect than the apes do.

III. FOSSIL APE-MEN

Although several fossil apes exhibit human characteristics, none of them has the enlarged brain characteristic of man. Intermediate between the fossil apes and living man were a number of creatures whose remains have been found in widely scattered regions of Europe, Asia and Africa. These remains are mostly pieces of skull, jawbones and teeth, although some other skeletal parts have been found. It is understandable that the fossil record of man's immediate ancestors is incomplete, for those animals were too intelligent to be caught in quicksands or tarpits, and, being primarily forest-dwellers, their dead bodies must have been quickly and completely devoured by other animals. Furthermore, at about this stage, burial customs arose involving the cremation of the dead. Most of the remains that have been found came from river sands—where death probably was an accident—or from caves. A survey of the existing evidence demonstrates that after the Miocene, various lines of human-like creatures arose, some much like modern man. We must conclude, however, that *the characteristics which distinguish man from the apes did not appear simultaneously in a single form, for although the ape-men are essentially human in some respects, they are apelike in others.*

Fig. 241. Restored skull of *Dryopithecus,* the fossil "oak ape," possibly the aneestor eommon to gorillas, chimpanzees and man. (Courtesy of the Ameriean Museum of Natural History, New York.)

Fig. 242. Front and side views of a reeonstructed skull of Peking man, *Sinanthropus pekinensis.* Note the massive bony ridges over the eyes, the low, retreating forehead, the protruding jaws and the absence of a chin. (Courtesy of the American Museum of Natural History, New York.)

1. The Java Ape-Man (*Pithecanthropus erectus*). One of the most primitive ape-men was *Pithecanthropus*, the Java ape-man whose remains were found in Pleistocene deposits on the banks of the Solo River in eastern Java. He had a brain capacity of about 940 cc., intermediate between modern man's 1200 to 1500 cc. and the 600 cc. of the gorilla. By studying casts of the interiors of these skulls, the contours and relative proportions of the various parts of the brain can be determined, and apparently *Pithecanthropus* had the part of the brain which controls speech, though whether he actually did speak is unknown. The frontal lobes of the brain, which were the last parts of the organ to appear in evolution, are smaller in *Pithecanthropus* than in man, but larger than in any living ape. All in all, Java man's brain was much larger and more convoluted than that of any of the primitive or living apes and was more human than simian. Reconstructions from the skeletal parts that have been found indicate that an adult was about 5 feet 8 inches tall, weighed 154 pounds and walked erect. His face was projecting and chinless, his jaws were massive and equipped with a huge set of teeth (although the canine teeth were not enlarged tusks as in the apes), he had a broad, low-bridged nose and a heavy, bony ridge over the eyes. It is probable that he had learned to use and make tools, for the rock strata bearing his remains also contain primitive stone implements. *Pithecanthropus* is believed to represent the remains of an archaic type which originated in the Pliocene and was once widespread throughout Asia.

Since 1891 when the first specimens of *Pithecanthropus* were found, excavations have turned up several more *Pithecanthropus* fossils, as well as the remains of a larger and apparently earlier ape-man, called *Meganthropus*, which is possibly a direct ancestor of the so-called Java man.

2. Peking Man (*Sinanthropus pekinensis*). Investigations during the early 1920's of certain limestone caves near Peking, China, revealed many animal fossils, among them two teeth which had belonged to a primitive ape-man of the middle Pleistocene, about 500,000 years ago. Dr. Black of the Peking Medical School gave the name *Sinanthropus pekinensis* to this creature. Further excavations in these caves revealed parts of more than forty individuals—males and females, old and young—of the same species. It is now possible to reconstruct fairly accurately what this ancient ape-man looked like. *Sinanthropus* had a skull much like that of *Pithecanthropus*, with heavy, bony ridges over the eyes, and a low, slanting forehead (Fig. 242). His jaw was massive, chinless and rather apelike, and his nose was broad and flat. The fact that the remains fall into two distinct groups, one composed of much larger specimens than the other, suggests that both sexes were represented—the larger fossils belonging to the males, the smaller to the females—and that the difference in size between them was much greater than at present. *Sinanthropus* had a distinctly larger brain than *Pithecanthropus*, the capacity ranging from 850 to 1300 cc. and averaging 1075 cc. The condition of the skulls with their bases broken open suggests that Peking man was a cannibal. As more specimens of Java and Peking men have turned up, it has become clear that the two were similar, probably

Fig. 243. Fragments of the skull of Piltdown man recovered from Piltdown Common. Could you deduce from these fragments what the man must have looked like? (See Fig. 247.) The object in the lower right corner is not a piece of skull, but a flint instrument found with the remains. (Courtesy of the American Museum of Natural History, New York.)

Fig. 244. Skull cap of Neanderthal man. No the heavy eyebrow ridges to the right and th extreme thickness of the bone. (Courtesy the American Museum of Natural Histor New York.)

representing two races of a single species. The anthropologist who has studied *Sinanthropus* most intensively, Professor Weidenreieh, found that in fifty-seven out of seventy-four charaeters of the skull, the two types are identical; in regard to thirteen charaeters there is some doubt and in only four charaeters are there distinct differences (one of these is the difference of size).

A curious anthropological story is that of *Gigantopithecus,* the "Hong Kong Drugstore Giant." In the late 1930's the investigator von Koenigswald bought a number of fossil teeth in a Chinese apothecary shop, some of whieh he identified as those of an orang-utan. Three of them, however, were larger than those of any known primate. Their diseoverer and Weidenreich believe them to be the remains of a giant ape-man which they named *Gigantopithecus,* related to the *Meganthropus* and the Java and Peking men.

3. Piltdown Man (*Eoanthropus dawsoni*). Between 1908 and 1915 a British lawyer named Dawson, whose hobby was colleeting fossils, found a number of skull pieees and a lower jaw in gravel pits on Piltdown eommon, Sussex (Fig 243). The gravel deposits date from the early Pleistoeene, and the name *Eoanthropus* (dawn man) seemed appropriate for the remains. Although the bones of the skull are thick—twiee as thick as those of modern man—and similar to those of the Java and Peking man, the skull is much like that of present-day man in other respeets: the forehead is high, there are no ridges over the eyes, and the brain eapaeity is about 1350 cc. But the lower jaw is quite like a ehimpanzee's, being chinless and having a projecting tusk for a canine tooth. In a number of other charaeters the jaw and teeth are intermediate between ape and man, although eloser to the human form than to that of the ape. It was onee thought that the skull and jaw actually belonged to two different animals, and were found merely by eoineidenee in the same gravel pit. But in another gravel deposit about a mile from the first, pieces of a skull like those of the original Piltdown discovery were found in elose conjunction with a large canine tusk like that of the Piltdown jaw. In 1936 parts of a similar skull were unearthed at Swanscombe in the valley of the Thames.

The relationship of the dawn man to modern man is in dispute. Its original describer, Professor Keith, regards it as an early offshoot from the main line of evolution to modern man, but Professor Hooton believes it to be closer to the direet evolutionary line leading to man than any fossil so far diseovered. In any event, the fact that this skull is like ours, yet dates from the early Pleistoeene, so that it was either eontemporary with or previous to the Java and Peking men, indieates that there were at least two evolutionary lines of manlike creatures during the Pleistocene.

IV. FOSSIL MEMBERS OF THE GENUS HOMO

Confusing to the beginning student of anthropology is the fact that a number of the fossil types discovered—Heidelberg man, Neanderthal man, Solo man, and others have been placed by their diseoverers in the same genus (*Homo*) as modern man, although some of them are no more manlike than the Java or Piltdown men.

4. Heidelberg Man (*Homo heidelbergensis*). Since the lower jaw is the only part of the so-called Heidelberg man that has been discovered, one cannot jump to conclusions in regard to his appearance. But the jaw itself is interesting. This fossil, buried under 80 feet of sand in a pit near Heidelberg, Germany, is remarkable for its massiveness. It is even larger than the jaw of Piltdown man and lacks a chin, but in the nature and arrangement of its teeth it is definitely human. The teeth are not exceptionally large, and the canines do not protrude beyond the other teeth, as they do in the Java and Piltdown men, as well as in the apes. The pulp cavities of the teeth are large, extending into the jaw, a condition found to some extent in Peking and Piltdown man, and markedly present in Neanderthal man, but also present in certain apes as well as in some modern human races. In many respects the jaw resembles that of Neanderthal man, and Heidelberg man is generally regarded as an ancestor of the Neanderthals. Since the fossils associated with the jaw are those of warm-climate animals—rhinoceroses and lions—Heidelberg man must have lived during one of the interglacial periods, but it is not clear whether it was the first or second of these; in any case he lived over 500,000 years ago.

5. Neanderthal Man (*Homo neanderthalensis*). The first human fossil discovered was found in 1856 in a cave of the Neander valley near Düsseldorf, and it was given the name *Homo neanderthalensis*, or Neanderthal man. The skull excited a lively controversy at first, some scientists correctly guessing it to be the remains of a primitive man, others guessing it to be the skull of a congenital idiot, and one surmising that it was simply the skull of a Russian soldier killed in the Napoleonic wars. Since that time similar skulls have turned up in widely separated parts of Europe, Asia Minor, North Africa, Siberia and the islands of the Mediterranean. These remains are always associated with a particular type of Stone Age culture known as the *Mousterian* (named after le Moustier cave on the bank of the Vézère River in France). Neanderthals lived in Europe for thousands of years during and after the third and final interglacial period (about 150,000 years ago), and became extinct only about 25,000 years ago.

Neanderthal man was between 5 and 5½ feet tall, and powerfully built; he walked upright, with bent knees. His skull was large and massive with a thick, bony ridge over the eyes, and a receding forehead (Fig. 244). His nose was broad and short, and he had almost no chin at all. Despite these rather apelike features, Neanderthal man had a brain as large as or larger than that of modern man, its capacity being about 1550 cc. The proportions of the parts of the brain, estimated from casts, indicate that, in general intelligence, he was probably quite similar to modern man, although his frontal lobes were smaller. Neanderthals lived primarily in caves, used fire, made flint weapons, and buried their dead reverently with food, ornaments and other helpful accessories.

6. Solo Man. On the banks of the Solo River in Java, just a few miles from the site where the *Pithecanthropus* remains were buried, have been found fossils of a second human type, which used both stone and bone implements. These men, considerably more advanced than *Pithecan-*

thropus, probably were descendants of that species. Eleven skulls of this new type (*Homo soloensis*) have been discovered since 1936, all with their bases smashed in, suggesting that Solo man, like his Peking cousin, was a cannibal who considered brains a delicacy. Like the Neanderthals, Solo men had a heavy ridge over their eyes and a receding forehead; the brain capacity was about 1300 cc., below the average for Neanderthals, but above that of the earlier Java man. Weidenreich has made a detailed study of these skulls and concludes that they are more primitive than Neanderthal skulls.

It is believed that the Australian bushmen are the present-day descendants of Solo man. In 1940 two skulls definitely of Pleistocene age were found at Keilor, near Melbourne, Australia, and although they have a large cranial capacity (nearly 1600 cc.), they are intermediate in other respects between Solo man and the modern aboriginal Australian.

7. Rhodesian Man (*Homo rhodesiensis*). Still another primitive skull, to which the name Rhodesian man has been given, was found in 1921 at Broken Hill, Rhodesia, in a large limestone cave. The skull, which was in an almost perfect state, has an extremely large eyebrow ridge and a receding forehead like a gorilla's, but a cranial capacity of about 1300 cc. The teeth are large, but definitely human rather than apelike, and are badly decayed—a condition never found in apes and only rarely in primitive man. The relationship of *Homo rhodesiensis* to the other extinct and living species of man is obscure; he lived either in the late Pliocene or the early Pleistocene, and in some respects is even more primitive than Java man.

8. Modern Man (*Homo sapiens*). The species *Homo sapiens* includes not only all the living races of man, but also some extinct ones, such as the Cro-Magnon. Just when *Homo sapiens* originated, and who his immediate ancestors were, are still unknown. Since Neanderthal man was more primitive than modern man, and lived, at the earliest, only about 150,000 years ago, it was argued for many years that our species arose recently, geologically speaking. But the discovery of additional fossils has indicated that *Homo sapiens* was a contemporary of Neanderthal man, and perhaps existed even before him.

The so-called **Galley Hill** man bears out this point. This fossil, found in 1888 in the Thames valley below London, is a nearly complete human skeleton, and the gravel pit containing it is of the Middle Pleistocene (about 500,000 years ago). Galley Hill man was short (5 feet 3 inches) and stocky, with no feature more apelike than some exhibited by living human races. His brain capacity was about 1400 cc. and the cast of his brain shows an essentially modern development of the various brain regions. The skull bones are quite thick, but the eyebrow ridges are not excessively large. The actual age of these remains is in dispute because the skeleton was removed before a qualified geologist could attest to the antiquity of the deposit. But the finding of the **Swanscombe** skull, which is essentially modern in shape and size, though differing in the greater thickness of the bones, in nearby Middle Pleistocene deposits renders likely the opinion of Sir Arthur Keith and Professor Hooton that

Galley Hill man also dates from the Middle Pleistocene. These investigators regard the Swanscombe and Galley Hill fossils as definitely of the species *Homo sapiens*, and believe them to have descended from the Piltdown species, which existed some 500,000 years ago, long before the oldest known Neanderthal men.

Since 1868 about 100 unmistakably *Homo sapiens* fossils, dating back 15,000 to 60,000 years, have been found in western and central Europe, especially in France. In the valley of the Vézère River in south central France the first well-preserved fossils of this type were discovered in the so-called **Cro-Magnon** rock shelters. At first these remains were thought to be representative of a single race, and were referred to collectively as the Cro-Magnon remains. Indeed, they do share certain characteristics, such as a long, massive skull without eyebrow ridges and with a prominent chin and high forehead, and a rather large brain capacity (as great as 1800 cc.). But further studies indicated that the fossils were not homogeneous enough to belong to a single race. Whatever their origins, they were probably contemporaries of the Neanderthal species, and may have hastened its extinction.

Excavations during the early 1930's, near Mt. Carmel in Palestine, disclosed a number of skeletons of Upper Pleistocene age, associated with Mousterian stone implements. The skeletons show an odd mixture of Neanderthal characteristics with others like those of the Cro-Magnon remains. The eye ridges are smaller than those of Neanderthal skulls, the forehead is less receding, the face is neither so large nor so long, the nose is narrower, and there is a fairly well-developed chin. The brain capacity varies from 1300 cc. to 1500 cc. and, in the development of the frontal lobes, resembles that of modern man more than that of the Neanderthal species. It appears that these remains are the result of hybridization between *Homo neanderthalensis* and early members of *Homo sapiens*, and many anthropologists believe that the Neanderthals did not become extinct in the strict sense of the term, but were absorbed by interbreeding with the various progressive and genetically dominant races of *Homo sapiens*. Neanderthals, in turn, shared many characteristics with the Java and Peking men, and probably descended from them, while Heidelberg man may represent an intermediate stage between the two.

Recent excavations in South Africa have revealed several fossils of *Homo sapiens* who died 20,000 or so years ago. And in the upper strata of the same caves near Peking in which the ape-man, *Sinanthropus*, was discovered, the remains of *Homo sapiens* of 75,000 years ago were uncovered. Among the latter, seven skeletons, belonging perhaps to members of the same family, were found together, apparently the victims of a human raid, for the skulls are all fractured. These are especially interesting because of the great variation among them, one of the men being like the European Cro-Magnon, one of the women resembling a modern Eskimo, and another a Melanesian. This heterogeneity suggests extensive hybridization among the various races of the time.

In contrast to the other continents, America seems to have been populated quite recently, during the last 20,000 years or so, and only

by *Homo sapiens*, for the few remains discovered there definitely belong to the same species as modern man.

According to Professor Hooton, all the present races of man—white, negroid and mongoloid—descended from Piltdown man, via the Swans-

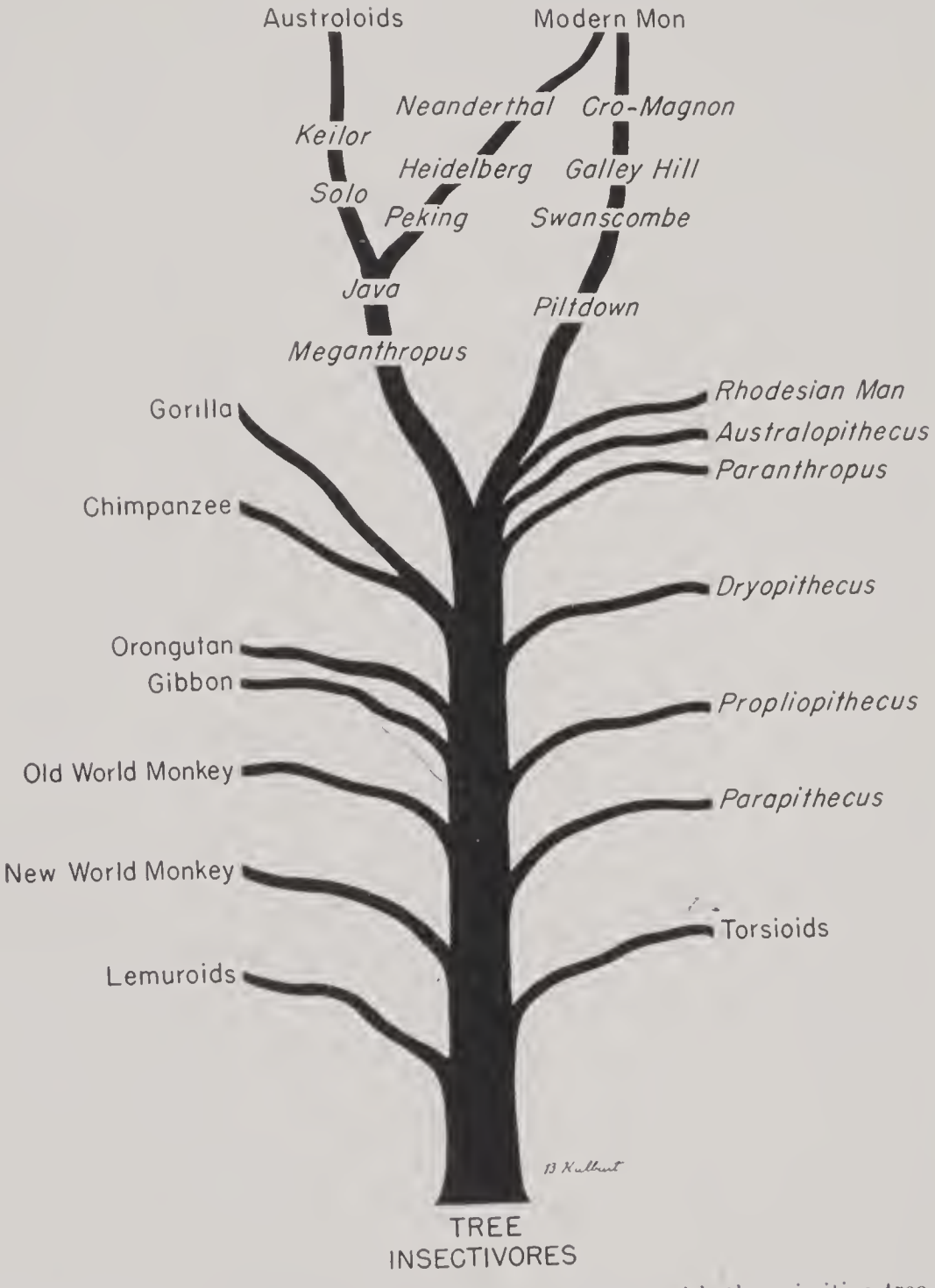


Fig. 245. An evolutionary tree of the primates, beginning with the primitive tree insectivores. The forms known only as fossils are indicated in italics.

combe, Galley Hill and Cro-Magnon lines, with a dash of Neanderthal, which, in turn, came from a separate line involving *Sinanthropus* and *Pithecanthropus* (Fig. 245). During this evolutionary process man has not increased greatly in height, and his frame has become less massive. He now stands completely erect, and his head is balanced on a relatively

slender neck, instead of being held in place by a massive set of neck muscles, and jutting forward from the shoulders. His skull capacity has increased, the forehead has become more vertical, the bony ridges over the eyes have diminished, and the face—particularly the jaws—has become smaller in relation to the rest of the skull (Fig. 246). Correlated with the reduction in the jaw size has been a reduction in the size and complexity of the teeth, and now there is a strong tendency for the third molars (the wisdom teeth) to be vestigial. What all this adds up to is that man, in common with the other animals, has adapted physically to changes in his way of life and in his environment. For hundreds of thousands of years his dangerous and physically demanding life required that he have a heavy, powerful body and strong jaws, with huge teeth for tearing and chewing his food. Then, as mutations for a larger brain and greater intelligence occurred, and were retained because of their survival value, he became less and less dependent upon physical strength for obtaining his food and escaping from, or overpowering, his enemies. In short, man has become a ground-dwelling, civilized animal, a fact which is reflected in the shape of his feet, his posture, his less rugged body and his comparatively delicate facial features.

V. CULTURAL EVOLUTION

Although most of the evidence of the path of human evolution comes from the actual fossils just discussed, some corroborative evidence comes from cultural implements, such as tools, weapons, cooking utensils and ornaments. The science called **archeology,** which is concerned with the cultural significance of such objects, is complex and fascinating, but unfortunately we can do no more here than indicate its importance.

Like fossils, the objects made and used by man, called **artifacts,** were deposited at widely separated times, and so are found in different layers of the soil, the later ones usually lying above the earlier ones. Thus, when fossils and artifacts are found together, and the date of the culture associated with the artifacts is known, the anthropologist is able to determine the age of the fossils at once.

At an early time man undoubtedly learned to pick up and use stones of a convenient size and shape, but not until the Middle Pleistocene, some 800,000 years ago, did it occur to him to chip pieces of flint to form hand axes. When it finally got under way, the culture characterized by this type of skill lasted 500,000 years; it is now called the **Lower Paleolithic** (paleo = old; lithic = stone), and it is believed to have been the culture of Peking, Java and Piltdown men. These men made their homes in caves and were hunters and food gatherers with no knowledge of agriculture or animal domestication. They did, however, understand the value of fire and knew how to make it. The association of certain kinds of axes and scraping tools with the Java and Peking fossils enables investigators to study the distribution of this type of ape-man, for similar artifacts, unaccompanied by skeletal remains, have been found in India and Burma.

In deposits dating from the third interglacial and the last glacial periods, different, more advanced tools have been found, and the culture

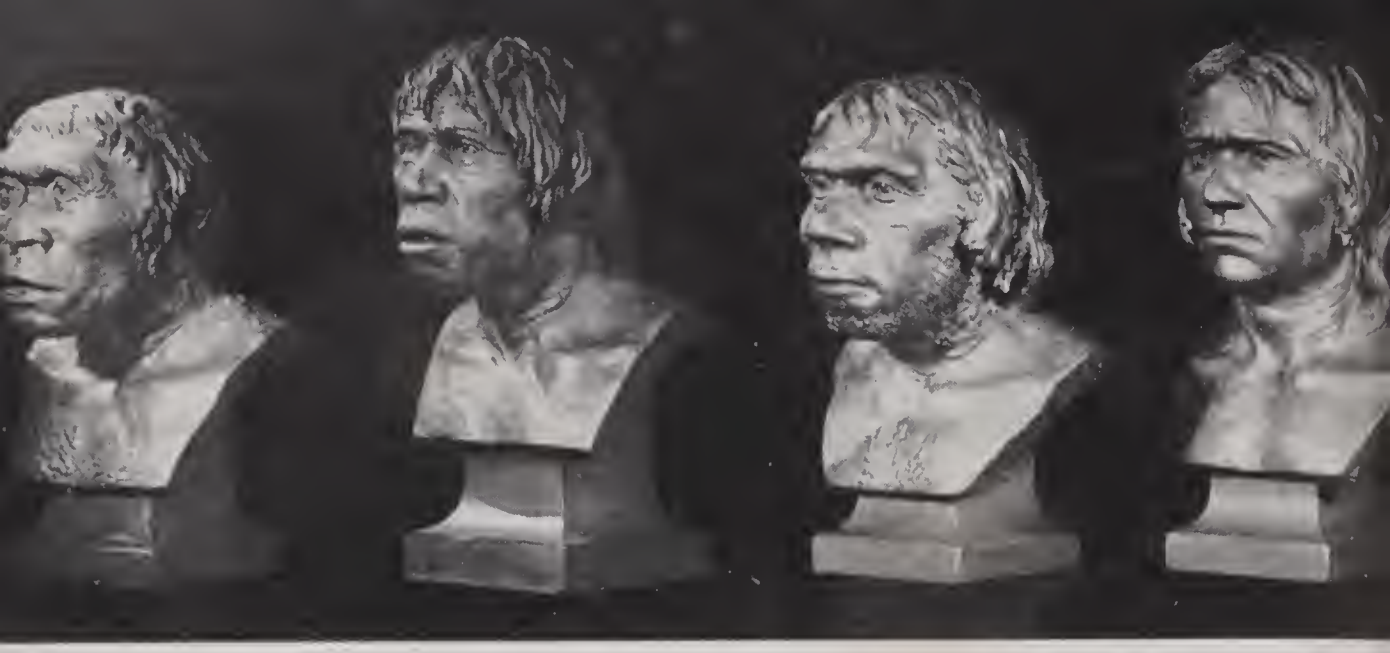


Fig. 246. Restorations by Dr. J. H. McGregor of what prehistoric men probably looked like. From left to right, the Java ape man, Piltdown man, Neanderthal man and Cro-Magnon man. (Courtesy of Dr. J. H. McGregor and the American Museum of Natural History, New York.)

Fig. 247. Restoration by Charles R. Knight of a group of Upper Paleolithic artists drawing animals on the wall of a cave. (Courtesy of the American Museum of Natural History, New York.)

Fig. 248. The art of Upper Paleolithic man; two reindeer from the wall of the cavern of Font-de-Gaume, Dordogne, France. (Courtesy of the American Museum of Natural History, New York.)

they represent has been named the **Middle Paleolithic.** The European branch of this culture, called the **Mousterian,** was associated with Neanderthal man. The implements of the Mousterian culture were made by chipping flakes from a piece of flint and then sharpening the edges by removing more flakes with a bone tool. The most common weapon seems to have been a triangular piece of stone, the forerunner of the spear and the arrowhead.

During the last 25,000 years of the fourth glacial period—that is, at the end of the Pleistocene—the culture characterized by the simple, chipped flint tools and weapons was replaced by another called the **Upper Paleolithic,** in which a new method for making implements was important. This method involved the removal of flakes from flint by means of steadily and carefully applied pressure, rather than by the force of blows, and resulted in long, slender, knifelike blades. Many of

these implements were elaborately and skillfully carved, in ways which not only enhanced their usefulness, but made them true objects of art. In addition to the skilled craftsmen responsible for such articles, there were at least a few excellent painters among the members of the Upper Paleolithic culture (Cro-Magnons and others), for the walls of caves in southern France bear paintings which are striking in their vitality and show a real understanding of the basic principles of design (Figs. 247, 248). The Upper Paleolithic people were also responsible for introducing bone needles, and probably invented the bow and arrow.

After such remarkable accomplishments the contributions of the **Mesolithic** or **Middle Stone Age** people seem insignificant. Indeed, the period is sometimes called the Dark Ages of the prehistoric era. It lasted 10,000 years and is important for marking the transition from the Paleolithic or Old Stone Age to the Neolithic. Mesolithic man was still a hunter and food gatherer, although he did domesticate the dog. His

tools were smaller and poorer in quality than those of his Upper Paleolithic predecessors, and there is no evidence that he continued the arts of painting and carving so highly developed by them. Perhaps, however, he attempted to write, for pebbles of this age have been found marked with red ochre dots, bars and crosses.

The **Neolithic** or **New Stone Age** culture, believed to have originated in the Near East, somewhere between Egypt and India, is characterized by implements which bear the marks of careful grinding and polishing. But much more important, it marks the beginning of agriculture and animal husbandry.* About 5000 B.C.,‡ then, man changed from a wandering hunter and food gatherer to a settled food producer. Next to speech, anthropologists consider these two accomplishments the most important steps in man's history. It was also during the Neolithic that pottery making was invented, and the remains of bowls, pitchers, and other utensils have been extremely helpful to archeologists, for each cultural group since that time has used certain peculiar methods in making and decorating such things. Other inventions of the ingenious Neolithic people are the dugout canoe and the wheel.

With the Neolithic age we come to historical times, for the oldest Egyptian and Mesopotamian cultures were Neolithic. The use of metals —first copper, then bronze (a copper-tin alloy)—for making vessels, tools and weapons began sometime between 4000 and 3000 B.C., and about 1400 B.C. men of the Near East initiated the Iron Age by mastering the technique of deriving iron from its ores.

VI. THE PRESENT RACES OF MAN

The differences between the various races of man living today are just as great as those between a number of other related animals generally regarded as different species, and a few anthropologists and geneticists —for example, Professor R. Gates (*Human Ancestry,* 1948)—argue that they are in fact different species. There can be no final answer to a question which is largely a matter of definition, but since the word "species" is usually used to imply interfertility, and since all the modern races of man are interfertile—as far as anyone knows—most biologists agree to consider them all members of *Homo sapiens.*

The term "race" is frequently misused for "nationality," and people talk about the white race, the Jewish race and the French race, when in reality they are discussing cultural factors. Scientifically speaking, the qualities which distinguish races are physical and physiological ones, similar to but smaller than those distinguishing the members of the larger taxonomic categories, such as phyla or classes. A race, then, is one of the great divisions of mankind, whose members share a certain combination of morphological and physiological features derived from their common ancestor.

* The earliest animals to be domesticated, after the dog, were the pig, sheep, goat and cow; the horse was not domesticated until much later.

† This date, like all others in the present discussion, cannot be considered as more than an approximation. Nor do the cultural periods apply to all the people in the world at any one time. The people in some parts of Asia and Africa are still in a Neolithic culture, and the aborigines of Australia, and the American Indians, were in an even earlier culture phase when the Europeans of advanced civilization arrived on those continents.

It should be clear by now that, ultimately, all the present races had a common origin, and that probably there is no such thing as a "pure" race. Anthropologists themselves are not agreed as to where the lines should be drawn, and the fact that any individual may be phenotypically so unlike his parents as to place him in a separate group from them indicates how inexact the science of physical anthropology must be. Furthermore, any particular quality, such as skin color, varies tremendously within each race, so that a member of the white race may have skin as dark as a typical Negro's, and a Chinese may have skin as white as a Caucasian's.

On the basis of a great many different qualities, however, we find that the people living today do tend to fall into one of three main categories, and the features in which they differ are as follows. Besides skin color, the color of the hair and eyes, the waviness and texture of the hair, the shape of the head and its features, the arrangement of the whorls and loops on the skin of the fingertips, and the proportions of the various parts of the body, are the most obvious anatomical factors to be considered. Anthropologists pay particular attention to the ratio between the breadth and length of the head. When measurements of a living person's head are made, this ratio is called the **cephalic index;** when measurements are made on a skull, the ratio is called the **cranial index.** By convention, a skull with a breadth less than 75 per cent of its length is called longheaded or **dolichocephalic,** one with a cranial index of 80 or more is said to be broad, roundheaded or **brachycephalic,** and a skull with a cranial index between 75 and 80 is said to be **mesocephalic.** Similarly, noses are classified according to the ratio of breadth to length —the **nasal index**—and the face is classified on the basis of the **facial index,** the ratio of length to breadth.

Some of the physiological characteristics in which the people of the world differ significantly are the chemistry of the blood, the rate of the basal metabolism and susceptibility to certain diseases.

9. The White Race. The white or Caucasian race probably includes a greater diversity of types than does either of the other two main races; in fact, so great is the diversity that only a few characteristics are shared by all members of the race. Generally speaking, however, the following traits seem to be typical of this division of the human family: a fairly light skin, ranging in color from light olive-brown through white to ruddy; medium to fine wavy or straight hair; fairly abundant facial and body hair; medium to thin lips; a moderately pronounced chin; and a broad pelvis. Women of the white race have hemispherical breasts and rather prominent buttocks.

There is no single method for classifying the members of the white race into subgroups, and no universally accepted opinion as to exactly how many subgroups there are. But most anthropologists agree that three main divisions do exist, called **Mediterranean, Nordic** and **Alpine.***

The Mediterranean group includes many Egyptians, Arabians, Portuguese, Spaniards, southern Italians and others, and is centralized between the Mediterranean and East Africa, the Indian Ocean and the Caspian Sea and between the Egyptian Delta and India. Typically, the

* There are different names for them; these terms and the descriptions that follow are based on C. S. Coon's *The Races of Europe* and E. A. Hooton's *Up from the Ape.*

people of this group have long heads, slender, slight bodies, olive or light-brown skin, black or brown hair that is straight or slightly wavy, and dark brown eyes. The Mediterranean race is probably the oldest and least specialized of any of the modern races.

The Nordic race, which is a partially depigmentized branch of the Mediterranean group, includes many Swedes, Norwegians, Englishmen, Scotsmen and north Germans. Its members are characterized by long heads, red, blonde or light-brown hair, blue or gray eyes, long, narrow faces with high, narrow noses, thin lips, ruddy skin and tall, slender bodies.

In contrast to the groups just described, our third main group, the Alpine, consists of broadheaded people whose ancestry includes Upper Paleolithic strains, and may well include some Neanderthal intermixture. Since the skulls of fossil men are longheaded almost without exception, we assume that brachycephaly occurred recently in human evolution; certainly it is not characteristic of the old Mediterranean stock. Unlike some Upper Paleolithic survivors, the Alpine people show a reduction in head and body size, being of medium stature, with round faces as well as heads, and of moderately stocky build. In hair and eye color they are usually intermediate between the dark Mediterraneans and the blonde Nordics. Members of the Alpine group are numerous in France, southern Germany, Switzerland and Greece, and are found in Asia as far east as the Pamir Mountains.

Two similar, composite white races are so important in the racial composition of modern Europe that they must be described. These races, called the **Armenoid** and the **Dinaric,** were produced by the interbreeding of the various main subraces and show a combination of their characteristics. The Armenoid is produced by a blending of Mediterranean and Alpine and is typically broadheaded, with a high, sloping forehead, high, pointed skull and hooked, convex nose. A great many of the residents of Turkey, Syria and Palestine are Armenoid. The Dinaric is a mixture of Mediterranean, Alpine and Nordic and, like the Armenoid, is roundheaded with a long face and prominent nose. Dinarics are common in Yugoslavia, the Austrian Tyrol, western Asia and Asia Minor, though they are found almost everywhere in the world.

10. The Negroid Race. It is generally believed that the original skin color of the human race was white, but just when the mutation for black or dark brown skin occurred in man's evolution no one knows. Nor is it known how the specialization of the Negro race came about or what relationships the Negroid subraces bear to each other. All we can do, then, is to observe and describe differentiations within the race.

Modern Negroids occur natively in two widely separated parts of the world: Africa and the islands of the Pacific from the Fijis to New Guinea. To explain this, anthropologists have postulated that the race originated in Asia and from there migrated east and west to those locations. Evidence that Negroids were once present along the southern and southeastern coasts of Asia is supplied by the many Negroid traits of several native tribes in India, Burma, Persia and Arabia. But the relationship between the Negros and the Negritos—the black pygmy race—is still undetermined.

Most Negroids have black, wooly or frizzy hair, dark brown or black skin, brown or black eyes, a low, broad nose, thick, puffy lips, a long head, sparse body and facial hair, relatively long shanks and forearms, a narrow pelvis, large feet and type O blood. The women usually have conical breasts and less protrusive buttocks than do white women.

The **Negritos** or **pygmies** are extremely short people, averaging less than 4 feet 9 inches in height, with round heads, narrow shoulders, pot bellies and short legs. They live in the Congo basin and in the interior of the Philippines, New Guinea, the Malay Peninsula and the Andaman Islands of the Indian Ocean. The Negritos are probably the most primitive culturally of living men, for they do not carry on agriculture, have no domesticated animals, and speak no language of their own. Many full-sized Negroes keep them as pets. It was thought at one time that they represent an earlier stage in the evolution of man, but there is no fossil evidence that man went through a pygmy stage; indeed, most of the prehistoric men were larger than the ones living today.

The **Oceanic Negroids** or **Melanesians** strongly resemble the Africans, but have thinner lips, less protrusive jaws, slightly lighter hair and skin, and their hair is less kinky. Less is known of these people than of most races, for they live in inaccessible places and are extremely unfriendly and cannibalistic.

The black-skinned race which originally occupied the island of Tasmania was destroyed by the white men who arrived there a little more than a century ago. The **Tasmanians** were quite short with wooly hair, short, flat noses, and abundant beards and body hair. They may have been an early offshoot of the Negritos, or they may have represented a type of Negro close to the primitive human stock. At any rate, they were living in a primitive Stone Age culture.

The **Bushmen** of South Africa are a rapidly vanishing race, which probably originated in that spot. They too are in a primitive Stone Age culture. Like the Negros farther north, they have black, kinky hair, and broad, flat noses, but their skin is much lighter—yellow to brown—and they average under 5 feet in height. The condition of steatopygia, which is an excessive accumulation of fat on the buttocks and thighs, is characteristic of these people, particularly of the women. Their extremely kinky hair is of a peculiar type, known as "pepper corn," because of the way it grows in tiny clumps of spiral coils, separated by bare spaces.

The **Hottentots** of South Africa resemble the Bushmen in many respects and are believed to have arisen by hybridization between Bushmen and whites.

11. The Mongoloid Race. The Mongolians are characterized by straight, coarse, black hair, yellow to yellow-brown skin, brown eyes, sparse beards and body hair, a broad face with projecting cheek bones, and a rather flat nose of medium breadth. Their most striking feature, of course, is the epicanthic fold of the upper eyelid, which is chiefly, but not wholly, responsible for the slanting appearance of their eyes. Actually, the eye slit itself is narrower and more slanting than that of the Caucasian eye. A high percentage of Mongolians have type B blood.

The classic Mongoloids, found in Mongolia, Eastern Siberia, and, slightly

mixed with other types, in China, Korea and Japan, are roundheaded and vary in height from short to moderately tall. In contrast, the Arctic Mongoloids—the **Eskimos**—are short, long headed people with a less pronounced epicanthic fold and more prominent cheek bones. The Arctic Mongoloids are found from Greenland to Northeastern Asia.

Composite races that are predominantly Mongoloid are the **Indonesians** and **American Indians.** The Indonesians, believed to have arisen by hybridization of the Mongoloids with Mediterraneans, Ainus and Negritos, are found in South China, Indo-China, Siam, Burma, Malaya and parts of the East Indies. Some of the Japanese belong to this group. The American Indians are the descendants of Mongoloids who entered America via Bering Strait in a number of waves of migration beginning some 20,000 years ago. Like the classic Mongolian, the Indians have round heads, prominent cheek bones and black, straight, coarse hair, but their skin has a reddish rather than a yellowish cast, the Mongolian eye fold is absent or small, and the nose is sometimes long, convex and high-bridged. The many subraces of the American Indian have not yet been thoroughly studied and classified, but even now it is apparent that they exhibit more variations in skin color, facial features and head shape than any other group of Mongolians. This is probably because by the time of the later invasions, Mediterraneans, Negritos and Australoids had interbred with the original Mongolian stock in Asia.

These, in brief, are the three main races of man, but we are not quite finished with the subject, for besides these three, and others which represent a mixture of them—such as the Polynesians, who are a composite of Caucasoid, Mongoloid and Negroid strains—there are at least three other groups which seem to belong to none of the three main races, and yet do not appear to be the result of hybridization. These are the **Ainus,** the **Veddoids** and the **Australoids.**

The Ainu is an ancient and remarkably primitive group which has lived for as far back as there is any record, on the islands of Northern Japan. They appear not to be of Mongolian origin, for they have white skin and wavy, black hair, which grows profusely on the face and body—hence they are usually called the "Hairy Ainu." And there is no trace of the Mongolian epicanthic fold. But there are geographic and historical reasons for doubting that they are Caucasian, and some anthropologists believe them to be Mongolians who underwent mutations which became well-established because of the former isolation of the Japanese islands.

The Australoids or Australian aborigines, have chocolate-colored skin, dark eyes, black hair, protruding jaws and receding chins. Because of their heavy eyebrow ridges, they are generally considered the most primitive of living races. But in spite of their many Negroid characteristics, they are not, apparently, of pure Negroid ancestry, for they have wavy rather than kinky hair which grows abundantly on both face and body. Their status, like that of the Ainu, has not been determined.

Throughout India and the East Indies, as well as in southeastern Arabia, occurs the third of our groups of unknown origin—the Veddoids. These uncivilized souls are dark, slender and long-headed; they have

broad noses and wavy hair, and the beard is moderately developed. In some ways, these people are similar to the Caucasian race, in others they resemble the Australoids, but what their true origin is, no one knows. What does seem quite certain is that in India, it is the intermixture with the Mediterranean race of the Veddoid element, rather than the Negroid, which is responsible for the dark skin color of so much of the population.

The science of physical anthropology teaches us, before anything else, that it is dangerous to generalize about the modern races of man. There is no evidence to show that any race is superior to any other, and the whole business of testing for such evidence is fraught with countless difficulties.

To begin with, an absolutely pure race is probably nonexistent, for the whole evolutionary history of man is one of intermixture. We know of the countless thousands of invasions from Africa and the Near East, from Mongolia and Siberia, from the Scandinavian countries, and so on, that have swept across the continents of Asia and Europe within historical times. Yet how complicatedly interwoven the human species must have been long before even the earliest historical period! This being so, it seems futile to test for racial superiority, for behind the skin color, eye shape and type of hair that are taken as a person's badge of race, innumerable ancestral strains may be masked. And it is these "hidden" strains which may be responsible for the traits of character and intelligence exhibited. The question then becomes, what race actually is being tested?

Even if it were possible to know exactly the ancestry of any group of people, a second difficulty would present itself—that of differentiating between hereditary traits and the influence of environment. Psychologists have found, for instance, that city children do much better on intelligence tests than country children. And the advantages of an adequate diet, the prompt correction of physical disabilities, and a feeling of security—in short, the benefits of a good invironment—are incalculable. There is simply no way of determining where the effects of such advantages stop and the effects of hereditary factors begin.

There are difficulties of language, too, to complicate the job of testing. Such words as "intelligence," "talent" and "morality" have no single, final meaning; each person interprets them according to his own background and education. And even if there were a way of establishing an objective definition, the qualities themselves are so complex, and dependent on so many physiological and psychological interrelationships that a comprehensive and true testing of them would still be well nigh impossible.

We have seen why the concept of racial purity is absurd. Is there any reason for supposing that a pure race would be superior if it did exist? On the contrary, the principle of hybrid vigor works just as well for human populations as it does for animals and plants. Thus, crosses between Indians and whites, Hottentots and whites, Chinese and Negroes often produce offspring which are taller, more vigorous and longer-lived than either of the parents.

At present, the only conclusion that anthropologists can offer concerning the capabilities of the various human races is that all of them have great potentialities and all have made important contributions to civilization. In time to come, investigators may find solutions for the problems of testing, and may be able to show correlations between certain racial strains and certain abilities. Whether that time comes or not, however, the person who can look upon the tangled web of humanity with any feeling of superiority at whatever his own little place in it may be, is indeed a victim of pride and prejudice.

QUESTIONS

1. What does it mean to say that an animal is unspecialized?
2. What are the ways in which man differs from the great apes?
3. Why is it incorrect to say that man came from monkeys? What did he come from?
4. Discuss how man's physical features have altered during his evolution from the ancestral lemuroids.
5. How does the science of archeology help that of anthropology?
6. Why was the year 5000 B.C. important for man? What innovations since that time do you consider the most significant for contributing to civilization?
7. List all the ways you can think of in which man's intelligence prevents his being as *biologically* successful as other animals. Do you think it is better for him to acquiesce to the biological demands, or to struggle against them? Begin by defining what you mean by "better," and be specific in your argument.
8. Do you think any of the known fossil primates should be called a "missing link?" If so, which one?
9. What is the relationship of Neanderthal to modern man?
10. Do you believe that the various races of men living today constitute one species or many? Why?

SUPPLEMENTARY READINGS

Coon, C. S.: *The Races of Europe.* New York, The Macmillan Company, 1939.
A definite but understandable treatise of the many subdivisions of the white race.

Gates, R. R.: *Human Ancestry.* Cambridge, Harvard University Press, 1948.
An advanced discussion of human evolution from the viewpoint that the present races of man are in fact different species.

Hooton, E. A.: *Up from the Ape.* Revised ed. New York, The Macmillan Company, 1945.
An amusing and informative presentation of the primates and of human evolution.

Osborn, H. F.: *Men of the Old Stone Age.* 3rd ed. New York, Charles Scribner's Sons, 1918.
An interesting, well-illustrated account of prehistoric man.

Romer, A. S.: *Man and the Vertebrates.* Revised ed. Chicago, University of Chicago Press, 1941.
A well-written, well-illustrated account of the evolution of the vertebrates in general and of man in particular.

CHAPTER 30

THE OUTCOME OF EVOLUTION: ADAPTATION

ONE OF THE most remarkable qualities of living things is the ease with which they get along wherever they happen to live. But the phrase "happen to live" is inappropriate, for it is not by accident that certain animals live in the trees, while others live on the ground, in the water, and so on. The reasons for this are implicit in the evolutionary story we have just been following. Now that we have seen what the forms of life are, and have some inkling of how they arose, it is time to consider the relationship of animals and plants to their environment —that is, their **adaptation.**

1. **Ecology.** The science which deals with this aspect of the biological world is called **ecology,** and basic to it are two concepts, the **ecologic niche** and the **habitat.**

The Ecologic Niche. The ecologic niche is an abstraction which includes all the physical, chemical, physiological and biotic factors that a given organism requires to keep alive. Specifically, the ecologic niche of a limpet is determined by such things as its need for a rock to cling to, a shallow, salt water environment, certain kinds of small plants to feed on, and so on. The ecologic niche is not a physical place, then, where a given organism resides, but the sum total of all the factors necessary for its survival. Each species—in fact, every member of each species—has its own ecologic niche, separate from that of every other one.

Habitat. In contrast, a habitat is a physical area, a certain specific part of the earth, air, soil or water. It may be as large as the ocean or a prairie, or as small as the under side of a rotten log or the intestine of a termite, but it is always a tangible region. Of course, more than one animal or plant may live in a particular habitat, and often several species occupy the same one.

2. **Biological Interactions.** Perhaps the one factor most basic to ecologic distribution, because it is basic to natural selection, is that living things reproduce many, many more offspring than the earth is capable of supporting. The potential reproductive rate of a given species under optimum conditions can be calculated from the ratio of males to females, the number of young per female, and the number of generations per year or century. For example, at a conservative estimate, one man and woman, with the cooperation of their children and grandchildren, could give rise to 200,000 progeny within a century, and a pair of fruit flies could be responsible for 3368×10^{52} offspring within a year. Since optimum conditions are never maintained, such biological catastrophes do not occur, but there are actual situations—India is an example—which indicate the tragedy implicit in the tendency towards overpopulation.

The sum of the physical and biological factors which prevent a species from reproducing at its maximum rate is termed the **environmental resistance,** and can be estimated by comparing the actual number of a given species in a certain region with the number there would be if the potential reproductive rate were maintained. Environmental resistance is often low when a species is introduced into a new territory, so that reproduction occurs at an alarming rate, as when the rabbit was introduced into Australia and the English sparrow and the Japanese beetle were brought into the United States. But as a species increases in number, the environmental resistance to it also increases, in the form of organisms that prey upon it or parasitize it, and the competition between the members of the species itself for food and living space.

Careful studies in the field have revealed some curious interrelationships between organisms, which illustrate the equilibrium of nature. For example, too few or too many rats are equally detrimental to a population of quail, for although rats eat quail eggs, they are eaten, in turn, by owls and hawks which prey upon the quail if the rat population is too small. A given species may be eliminated if too many of its normal predators are removed. Thus, when an effort was made in the Kaibab National Forest, north of the Grand Canyon, to protect the deer population by eliminating wolves and mountain lions, the deer increased so rapidly that there was no longer enough grass and leaves to support them through the winter, and a tremendous number died of starvation.

3. Structural and Physiological Adaptations. Because so many members of every species are struggling for a portion of the earth's food and space, there is a tendency for the members of any new group of organisms to spread out and occupy as many different regions as they can reach and as will support them. The type of distribution, involving the evolution from a single ancestral species, of a variety of forms which occupy different habitats, is called **adaptive radiation.** It is obviously advantageous in enabling the animals to tap new sources of food and to escape some of their enemies. The placental mammals provide a classic illustration of the process, for from a primitive, insect-eating, five-toed, short-legged creature that walked with its soles flat on the ground, all the great variety of present-day mammals evolved (Fig. 249). Thus there are dogs and deer, adapted for a terrestrial life in which running rapidly is important; squirrels and primates, adapted for an arboreal life; bats, equipped to fly; beavers and seals, capable of maintaining an amphibious existence; the strictly aquatic whales and sea cows; and moles, gophers and shrews, tunneling (fossorial) animals, able to live underground.

Many of the animals occupying the same type of habitat have similar structures which make them superficially alike, even though they may be only distantly related. This is due, as we have already seen, to the process of **convergent evolution,** and is splendidly illustrated by the similarity of the dolphin and porpoise (which are mammals) and the old, extinct ichthyosaurs (which were reptiles) to the fish; all of them evolved a streamlined shape and dorsal fins useful for life in the sea (Fig. 250). And moles and gophers, in adapting to a fossorial life, have evolved

similar fore and hind leg structures, although the moles are insectivores and the gophers are rodents.

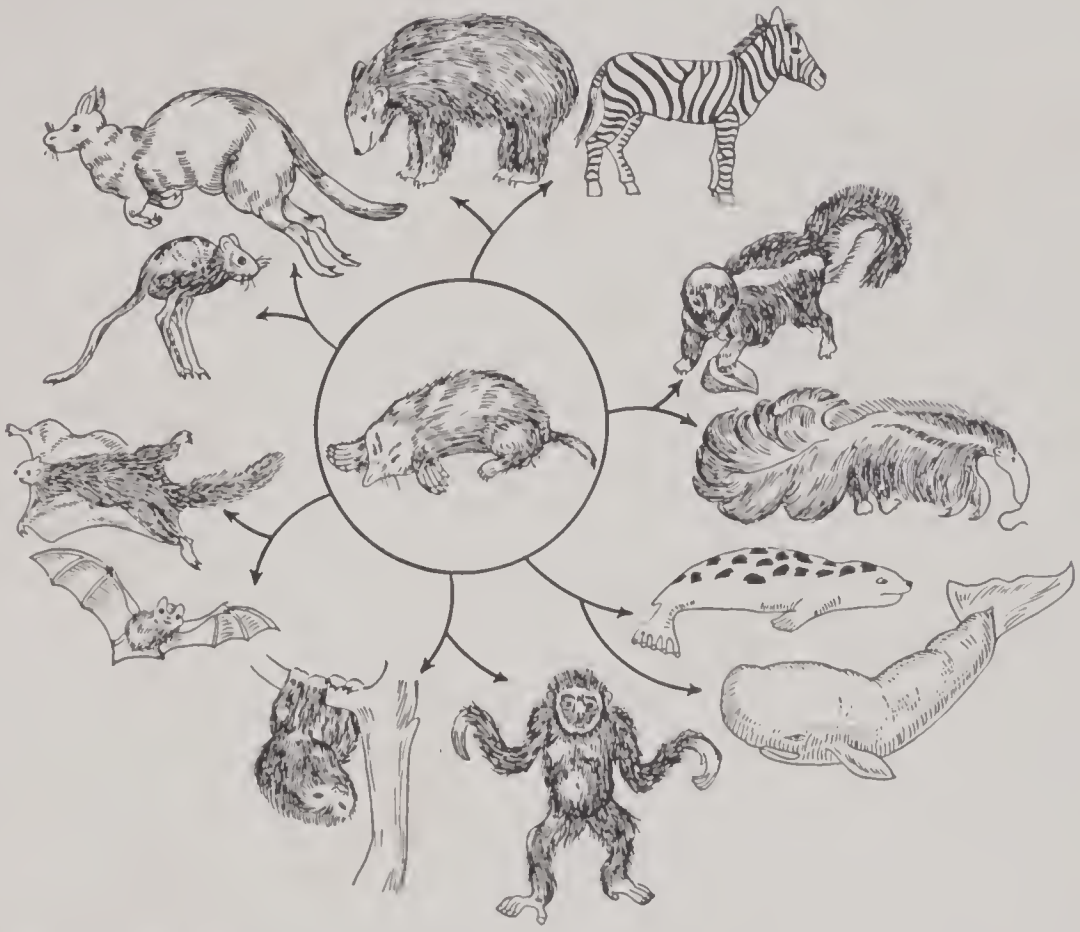


Fig. 249. Adaptive radiation. All the various mammals shown have evolved from the common ancestor shown in the center, but have become adapted to a wide variety of environments. (Hunter and Hunter: College Zoology.)

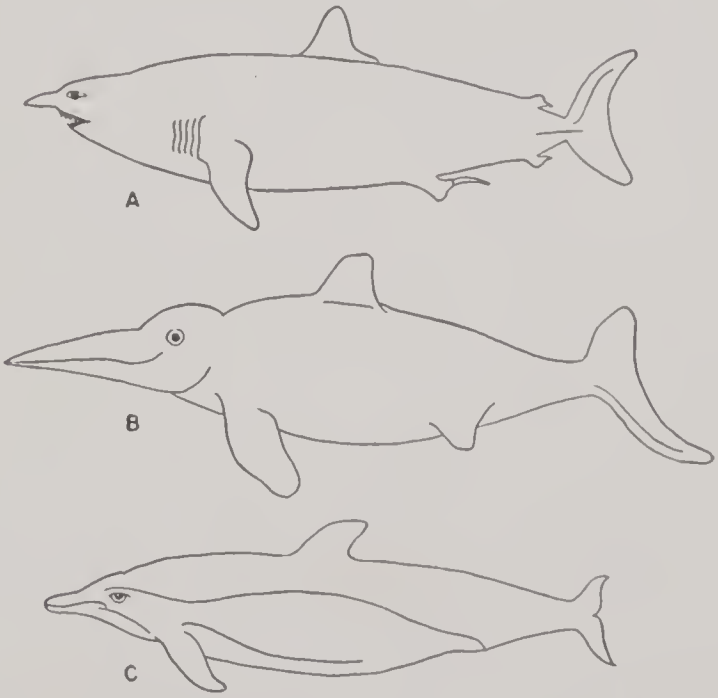


Fig. 250. Convergent evolution. *A*, Shark; *B*, ichthyosaur (a fossil reptile); and *C*, dolphin (a mammal), all of which have a marked superficial similarity because of their adaptation to the same environment. (Hunter and Hunter: College Zoology.)

In some of the modern animals the specialized adaptation to a certain way of life is just the latest stage in a series of adaptations. Thus both

man and the baboon, whose original ancestor was a ground-dwelling animal, have returned to the ground and readapted to walking rather than to climbing trees. Often readaptation is a complicated process. The present-day Australian tree-climbing kangaroos descended from an original marsupial ancestor, which is believed to have been a ground form. From these ground-dwellers, other forms evolved which took to the trees and developed limbs adapted to tree climbing—or perhaps the order of events was reversed—first the evolution of specialized limbs, and then the tree-dwelling mode of life. At any rate, these animals, in turn, eventually left the trees and became readapted to a ground life, where the walking type of leg became lengthened, strengthened and adapted for leaping, as in other kangaroos. But, finally, some of these kangaroos went back to the trees, although by that time their legs were so highly specialized for leaping that they could not be used for grasping. Consequently, the living tree-kangaroos have to climb like bears, by bracing their feet against the tree trunk. By comparing the feet of existing Australian marsupials, all the stages in this complicated, shifting process can be seen.

4. Physiologic Adaptations. Since one of the major struggles between organisms stems from the competition for food, a mutation enabling an animal to use a new type of food is extremely advantageous. This may be accomplished in a number of ways—for example, through the formation of a new digestive or energy-liberating enzyme. It was a mutation resulting in the latter which enabled the sulfur bacteria to obtain energy from hydrogen sulfide, a substance which is poisonous to almost all other organisms.

Another type of helpful mutation is that which decreases the growing season of a plant, or the total length of time required for an insect to develop, thereby enabling the organism to survive farther from the equator, where the summers are shorter.

Although the range of temperature in the universe is from —273° C. (absolute zero) to well over 6000° C. (on the sun), life as we know it can occur only within a temperature range of a few degrees below zero and about 60° C., each species having an optimum temperature between those two. Therefore, any mutation that increases the limits of temperature tolerance for a species may enable it to inhabit a new part of the world. Similarly, since most organisms can survive only within a comparatively narrow humidity range, a mutation would be helpful which enabled a species to tolerate a moister or drier environment.

Another sort of physiologic adaptation is demonstrated by the whale. Marine animals are usually adapted to survive in a particular pressure range, so that surface animals are crushed by the terrific pressures of the deep, and the deep-sea animals burst when brought to the surface. But the whale is able to withstand great changes in pressure, and thus can dive to depths of 4000 feet without injury.

5. Color Adaptations. Adaptations for survival are evident in the color and pattern of plants and animals as well as in their morphology and physiological processes. Ecologists recognize three types of color adaptation: concealing or **protective coloration,** which enables the organism to blend with its background and so be invisible; **warning coloration,**

which consists of bright, conspicuous colors and is assumed by poisonous or unpalatable animals to warn their potential predators not to eat them; and **mimicry,** in which the organism resembles some other living or nonliving object—a twig, leaf, stone, or perhaps some other animal which, being poisonous, has warning coloration.

In some cases concealing coloration is assumed by an animal which wishes to escape the notice of a potential predator; in other cases it is assumed by a predator in order to be invisible to his potential prey. Examples of such coloration are innumerable and include the white coat of arctic mammals and the stripes and spots of tigers, leopards, zebras and giraffes, which, although conspicuous enough in the zoo, blend imperceptibly with the moving patterns of light and dark, typical of the jungle. Some animals, such as the frog, chameleon and many shrimps, crabs and fish, can change their color and pattern as they move from a dark to a light background, or from one that is uniform to one that is mottled.

To demonstrate experimentally that these concealing colorations do have survival value, investigators devised an experiment involving variously colored grasshoppers tied to small stakes in different plots of soil—some sandy, some grass-covered and some covered with dirt. After the plots had been exposed to chickens or wild birds for awhile, the experimenters found that a significantly larger number of the grasshoppers which matched their respective backgrounds, survived.

When an animal is equipped with poison fangs, a stinging mechanism or some chemical which gives it a noxious taste, it is to its advantage to have the fact widely advertised, and in fact, many animals of this sort do have warning colors. An interesting example is a species of European toad with a bright scarlet belly. The toad has certain chemicals in its skin which makes it extremely unpalatable, and whenever a potential predator, such as a stork, swoops over a congregation of the toads, they flop on their backs, exposing their scarlet bellies as a warning. Storks and other birds apparently become conditioned by the association of the red color with the bad taste, and avoid the toads assiduously.

Other animals survive by mimicking one of these protectively colored animals—for instance, some harmless, defenseless and palatable animals are identical in shape and color with a poisonous or noxious animal of quite a different family or order, and, being mistaken for it by predators, are left alone. Many tropical insects have evolved this type of protection. The arrangement is only possible where there are many more genuinely disagreeable or dangerous organisms than forms which mimic them, for, obviously, if half the time or more, a predator finds that animals with a particular shape and color are palatable, he will not become conditioned to avoid them.

Color and pattern are also used to attract other organisms when that is necessary for survival. The red and blue ischial callosities of monkeys, and the gay, extravagant plumage of various birds apparently have an attraction for members of the opposite sex. And vividly colored flowers seem to draw bees and birds whose activities are helpful to the plants in insuring pollination.

These are but a few of the special adaptations which enable plants and animals to obtain food, escape enemies and carry on the processes of reproduction. Each living form benefits from the accumulated adaptations of its ancestors, which the continuing process of natural selection is constantly perfecting. Alone of all the animals, man seems to be making a determined effort not to adapt to his environment, but to adapt the environment to himself.

6. Terrestrial Life Zones. In addition to what might be called their horizontal distribution, organisms are distributed vertically as well, some habitats being on the surface of the earth, others beneath it, and so on.

This vertical distribution is strikingly apparent when one drives from the floor of the San Joaquin Valley of California into the Sierras. The floor of the valley is semidesert (it would be much more arid were it not for extensive irrigation), with vegetation consisting of sagebrush, cactus, yucca, thorny shrubs and short-lived annual plants, capable of completing their entire life cycle—from seed through the adult plant and flowers, to seed—in the few weeks following a rain. Its fauna is made up of a few birds, mice, lizards and snakes. This region is called the **Sonoran.**

As one ascends the foothills the next zone is the colder and moister **Transitional** region, consisting of deciduous forests, such as oaks and beeches, and an animal population of blue jays, skunks, deer and meadow mice.

Still higher is the **Hudsonian-Canadian** region of evergreen forests, with pines and firs, and such animals as the woodchuck, porcupine, rabbit, fox and wolf.

Above the timberline is the **Arctic-Alpine** region, snow-clad for half the year or more. The vegetation here consists of mosses and lichens, plus a few low shrubs, and the fauna is comprised of a few insects, rosy finches, conies and mountain goats.

In equatorial areas, along the coast near sea level, is a region called the **Tropical Rain Forest,** lower than the Sonoran. Those like the coasts of Mexico and Ecuador, and the Amazon and Congo valleys, are characterized by a profusion of luxuriant, broad-leaved trees and vines, and by monkeys, exotic birds, butterflies, beetles and spiders, which thrive in its hot, humid climate.

These life zones are differentiated on the basis of such things as the amount of annual rainfall, the temperature range and the length of the growing season, which determine the types of vegetation; the plants, in turn, plus the physical factors, determine the fauna of the region.

As one travels from the equator in the direction of either pole, the same series of life zones can be differentiated as exist at various altitudes of the same latitude. Thus one finds the Sonoran region in the Mexican plateau and southwestern United States, the Transitional region in the central and eastern United States,* the Hudsonian-Canadian region in southern and central Canada, and the Arctic-Alpine in northern Canada and Alaska.

* The prairie regions of the West cannot support forests because the long dry spells prevent tree seedlings from becoming established.

7. Marine Life Zones. Like the land, the ocean has clearly demarcated regions characterized by different physical conditions, and consequently inhabited by quite different plants and animals. These are as follows: (1) the **tidal zone,** the beach between the high and low tide marks; (2) the **shallow sea,** the region lying over the continental shelf and extending out to a depth of about 500 feet; (3) the **pelagic,** the open ocean down as far as sunlight can penetrate (some 500 to 1000 feet); and (4) the **abyssal** region, the area of the ocean beyond the continental shelf and beneath the pelagic.

The tidal zone is one of the most favorable of all the habitats in the world, and many biologists believe that life originated here. The abundance of light, water, oxygen, carbon dioxide and minerals makes it extremely salutary for plants and, by assuring them sufficient food, makes it an excellent habitat for animals. The plants of the region are primarily a wide variety of algae and a few grasses. Members of every phylum of the animal kingdom are present, too, a situation which prevails only here and in the nearby shallow sea. There is keen competition among the plants for space, and among the animals for space and food, so the forms living here have to evolve special adaptations in order to survive.

Since the intertidal zone is exposed to air twice daily, its inhabitants have had to develop some form of protection against drying up. Some animals avoid this by simply burrowing into the damp sand or rocks until the tide returns; others have developed shells which can be closed, and so retain a portion of water. Many plants are equipped with a jelly-like substance (agar) which absorbs and holds large quantities of water while the tide is out.

One of the outstanding conditions of this region is the everpresent action of the waves, which the organisms living on a sandy or rocky beach have had to find ways of resisting. The various sea weeds all have tough, pliable bodies, able to bend with the waves without breaking, while the animals are either encased in hard, calcareous shells, like those of the molluscs, bryozoa, starfish, barnacles and crabs, or are covered with a strong, leathery skin that can bend without breaking, like that of the sea anemone and octopus.

The shallow sea region is also thickly populated, for it has plenty of light and other things required by plants. The absence of the periodic exposure to air, and the diminished wave action permits many animals to live here that could not survive in the tidal zone. Many species of fish exist here, and many single-celled algae; the larger sea weeds, which need a substrate, are found only in the shallower parts of the region.

The pelagic region, distinguished by the presence of sunlight and the absence of a substrate, is populated by "swimmers" and "floaters." There are no large sea weeds here (except occasional pieces torn from their anchorage by waves and washed to sea as in the "Sargasso Sea"), and fewer microscopic algae than in the zones nearer shore. There are many varieties of microscopic animals: protozoa, such as foraminifera and radiolaria; small crustacea; and the larvae of many forms. A few large animals live here—the jellyfish, the Portuguese man-of-war, the

squid, plus a few fishes and whales. (Some whales feed upon the microscopic forms of life and are equipped with strainers to remove them from the water; others, preying upon fish, squids and other whales, are equipped with teeth.)

Below the pelagic is the abyssal region, characterized by the absence of light and the consequent absence of plants. The waters are quiet and cold, and the pressure is stupendous. The animals here must feed upon each other or on the bodies of dead plants and animals that are constantly settling down from above. Most of the fish of the abyssal region are rather small and peculiarly shaped, and many are equipped with luminescent organs, which act as lures for the forms preyed upon. The majority of the deep-sea creatures are related to shallow-sea forms, and they must have migrated to their present habitat recently, geologically speaking, for none is older than the Mesozoic.

Since the number of any species in these vast depths is small, reproduction is more of a problem than in any other region, and some animals have evolved a curious adaptation to ensure that reproduction will occur. At an early age the male becomes attached to and fuses with the head of the female, where he continues to live as a small (inch-long) parasite. In due course, he becomes mature, and, when the female lays her eggs, he releases his sperm into the water to fertilize them.

The bottom of the sea is a soft ooze, made of the organic remains and shells of foraminifera, radiolaria and other animals. Many invertebrates live on the ocean floor at great depths, and are usually characterized by thin, almost transparent shells, whereas the related shallow-water forms, exposed to wave action, have thick, hard shells. Apparently even the greatest "deeps" are inhabited, for tube-dwelling worms have been dredged from depths of 24,000 feet, and sea urchins, starfish, bryozoa and brachiopods have been found at depths of 18,000 feet.

With the discussion of distribution we return to the subject which formed our point of departure in the introductory chapter—the earth with its abundance and diversity of living things. As we think of the panorama now, it should be more substantial, supported by what we know of the ways in which living things differ from inanimate objects, the kinds of organisms there are and their relationships, the structure and function of various animals and plants, the processes of evolution and the distribution of organisms over the earth.

However useful and interesting these facts about the animate world may be, they are equally—perhaps we should say particularly—valuable simply as a base for other investigations. In the first chapter we found that it is possible to think of the world and the universe as existing on three different levels, and that the solid, familiar level of the earth with its plants and animals is dependent upon a mysterious substrate of atoms and electrons, and is the foundation, in turn, of a mysterious superstructure—the world of human affairs. In this book it was our business to survey the outstanding, broad divisions of the living, solid level; above all else, we should be left with an impression of how closely related are the three levels, of how tenuous is the line between, for instance, the biochemistry of the brain cells, the anatomy and physiology

of the brain (and the entire body) and such phenomena as thought and emotion. This is to suggest that whether one is interested in first causes or final effects the science of biology provides an excellent basis for a liberal education, but that it is only a beginning.

QUESTIONS

1. Explain the concept of the ecologic niche. Define the ecologic niche of a bee.
2. What is a habitat?
3. What is environmental resistance? How would you measure the environmental resistance to rabbits on Long Island?
4. Contrast adaptive radiation and convergent evolution.
5. Discuss the main types of adaptation exhibited by mammals.
6. What determines the extent of the vertical life zones?
7. Compare the adaptations made by barnacles, snails and starfish which enable them to survive in the intertidal zone.
8. What value has biology for the average person? How do you think it compares with history, philosophy and psychology as a point of departure for trying to understand the world? What are the limitations of the "biological viewpoint?"

SUPPLEMENTARY READINGS

Allee, W. C., and others: *Principles of Animal Ecology*. Philadelphia, W. B. Saunders Company, 1949.
The definitive treatise on animal ecology, detailed and thorough, but easily understandable.

Cott, H. B.: *Adaptive Coloration in Animals*. Oxford, Oxford University Press, 1940.
A wonderfully illustrated account of animal camouflage.

Elton, C.: *Animal Ecology*. New York, The Macmillan Company, 1937.
A delightfully written account of the relation of animals to their environment.

Pearse, A. S.: *Animal Ecology*. 2d ed. New York, McGraw-Hill Book Company, Inc., 1939.
A more technical presentation of animal adaptations.

Weaver, J. E., and Clements, F. E.: *Plant Ecology*. 2d ed. New York, McGraw-Hill Book Company, Inc., 1938.
An interesting though detailed presentation.

APPENDIX

A SURVEY OF THE PLANT AND ANIMAL KINGDOMS

THE SYSTEM of classifying animals and plants—cataloguing them by phylum, class, order, family, genus and species—was discussed in Chapter 5. In the synoptic survey given here the phyla within the kingdoms and the classes within the phyla are arranged in the order of increasing complexity as far as possible; but since evolution has proceeded in a branching fashion, it is impossible to arrange the animals and plants rigidly in order, from simple to complex. The numbers given are estimates of the known species in the phylum; for many of the groups there are many additional species as yet undescribed.

I. THE PLANT KINGDOM

Organisms classified as plants usually have stiff cell walls and chlorophyll.

1. Phylum Thallophyta. The simplest plants, without true roots, stems or leaves; the body is either a single cell or an aggregation of cells with little differentiation into tissues. (107,000)

Subphylum Algae. Thallophytes with chlorophyll and autotrophic nutrition.

Class Cyanophyceae. The blue-green algae, with no distinct nuclei or chloroplasts; probably the most primitive of existing plants.

Class Chlorophyceae. The green algae, with definite nuclei and chloroplasts.

Class Phaeophyceae. The brown algae, with multicellular, often large bodies—the large seaweeds.

Class Rhodophyceae. The red algae. Multicellular, usually marine plants, sometimes impregnated with calcium carbonate.

Subphylum Fungi. Thallophytes without chlorophyll and with saprophytic or parasitic nutrition.

Class Schizomycetes. The bacteria.

Class Myxomycetes. The slime molds. The body consists of a mass of protoplasm containing many nuclei, but not sharply divided into cells. Movement by ameboid motion.

Class Phycomycetes. The algal fungi—bread molds and leaf molds.

Class Ascomycetes. The sac fungi—yeasts, mildews and cheese molds.

Class Basidiomycetes. Mushrooms, toadstools, rusts and smuts.

Class Fungi Imperfecti. A heterogeneous collection of fungi in which sexual reproduction is unknown, and which are not easily assigned to one of the other classes.

2. Phylum Bryophyta. Multicellular plants, usually terrestrial, with a marked alternation of sexual and asexual generations. The prominent

plant is the gametophyte (sexual generation), on which the sporophyte is dependent. (23,000)

Class Hepaticae. The liverworts. Usually simple, flat plants, living in moist, shady places.

Class Musci. The mosses. The gametophyte plant has an erect stem, and leaves arranged in a spiral.

3. Phylum Pteridophyta. Multicellular, terrestrial plants, with true roots, stems and leaves, a well-developed vascular system, and with alternation of sexual and asexual generations. The prominent plant is the sporophyte; the gametophyte is free-living and tiny. (9000)

Class Psilophytales. The extinct, ancestral pteridophytes.

Class Equisetineae. The horsetails.

Class Lycopodineae. The club mosses and quillworts.

Class Filicineae. The ferns.

4. Phylum Spermatophyta. Multicellular plants with well-developed roots, stems and leaves; vascular systems differentiated into phloem and xylem. The dominant plant is the sporophyte; the gametophyte is small and dependent on the sporophyte. This group includes the trees, shrubs and herbs, commonly called the seed plants. They differ from the pteridophytes in reproducing by seeds, and in having pollen tubes. (150,000)

Class Gymnospermae. The conifers, cycads and most other evergreen trees and shrubs. Spermatophytes without true flowers or ovules, the seeds being born naked on the surface of the cone scales.

Order Cycadofilicales. The seed ferns—the most primitive of the spermatophytes—known only from fossils (Late Paleozoic Era).

Order Cycadales. The cycads, the most primitive living spermatophytes, found in tropical and subtropical regions.

Order Ginkgoales. The ginko, or maidenhair tree, is the only living member of this group.

Order Cordaitales. Extinct, large-leaved evergreen trees. Fossil remains of these have been found in deposits from the Devonian to the Permian.

Order Coniferales. The conifers, the common evergreen trees and shrubs, with needle-shaped leaves.

Order Gnetales. Climbing shrubs or small trees found in tropical and semitropical regions, with many characteristics in common with the angiosperms.

Class Angiospermae. Flowering plants, with seeds enclosed in an ovary.

Subclass Dicotyledoneae. Most flowering plants. Embryos with two cotyledons or seed leaves; vascular bundles in a ring in the stem; leaves with netlike venation; flower parts (sepals, petals, stamens and carpels) in fives, fours or twos.

Subclass Monocotyledoneae. The grasses, lilies and orchids. Leaves with parallel veins, stems in which the vascular bundles are scattered, and flower parts in threes or sixes. The embryo has only one seed leaf.

II. THE ANIMAL KINGDOM

Organisms classified as animals usually lack stiff cell walls, and never have chlorophyll; nutrition is either holozoic or parasitic.

1. Phylum Protozoa. Microscopic, unicellular animals, which sometimes aggregate in colonies. Some are free-living; others are parasitic. (15,000)

Class Flagellata. Protozoa which move by whiplike protrusions of protoplasm called flagella. Primitive animals, probably the group most closely related to the one-celled plants.

Class Sarcodina. Protozoa which move by pseudopodia.

Class Sporozoa. Parasitic protozoa which reproduce by spores and have no method of locomotion.

Class Ciliata. Protozoa which move by means of cilia.

2. Phylum Porifera. The sponges, both fresh-water and marine. The lowest of the many-celled animals, resembling in many respects a protozoan colony. The body is perforated with many pores to admit water, from which food is strained. (3000)

3. Phylum Coelenterata. Radially symmetrical animals with a central gastrovascular cavity. The body wall consists of two layers of cells, in the outer of which are stinging cells, nematocysts. (4500)

Class Hydrozoa. Hydra-like animals, either single or colonial. There is usually an alternation of a hydra-like (asexual) generation with a jellyfish (sexual) generation.

Class Scyphozoa. True jellyfishes.

Class Anthozoa. The corals and sea anemones, which have no alternation of generations. The digestive cavities of these animals are divided by mesenteries to increase the effective surface.

4. Phylum Ctenophora. The comb jellies or sea walnuts. These animals lack the stinging capsules of coelenterates and move by means of eight comblike bands of cilia. (100)

5. Phylum Platyhelminthes. The flatworms, with flat, and either oval or elongated, bilaterally symmetrical bodies, and three cell layers. The excretory organs are flame cells. There is a true central nervous system. (6000)

Class Turbellaria. Nonparasitic flatworms with a ciliated ectoderm.

Class Trematoda. The flukes, parasitic flatworms with nonciliated ectoderm, and one or more suckers. Many are internal parasites with complicated life cycles.

Class Cestoda. The tapeworms, parasitic flatworms with no digestive tract; the body consists of a head and a chain of "segments" or individuals which bud from the head.

6. Phylum Nemertea. The proboscis worms. Nonparasitic, usually marine animals with a complete digestive tract and a protrusible proboscis armed with a hook for capturing prey. The lowest animals with a blood vascular system. (400)

7. Phylum Nematoda. The roundworms. An extremely large phylum. Characterized by elongated, cylindrical, bilaterally symmetrical bodies; they live as parasites in plants and animals, or are free-living in the soil or water. (80,000)

8. Phylum Acanthocephala. The hook-headed worms. Parasitic worms with no digestive tract and a head armed with many recurved hooks. (100)

9. Phylum Chaetognatha. Free-swimming marine worms, with a body

cavity (celom) which develops from pouches of the digestive tract (as in the echinoderms and lower chordates). (30)

10. Phylum Nematomorpha. The horsehair worms. Extremely thin, brown or black worms about 6 inches long, resembling a horsehair. The adults are free-living, but the larvae are parasitic in insects. (200)

11. Phylum Rotifera. Small, wormlike animals, commonly called "wheel animalcules," with a complete digestive tract, flame cells, and a circle of cilia on the head, the beating of which suggests a wheel. (1200)

12. Phylum Gastrotricha. Microscopic, wormlike animals resembling the rotifers, but lacking the crownlike circle of cilia. (100)

13. Phylum Bryozoa. "Moss" animals. Microscopic organisms, usually marine, which form branching colonies. Characterized by a U-shaped row of ciliated tentacles, the lophophore, by means of which they capture food. (1200)

14. Phylum Brachiopoda. The lamp shells. Marine animals with two hard shells (one dorsal and one ventral), superficially like a clam. They obtain food by means of a lophophore. (200 at present; 3000 extinct)

15. Phylum Phoronida. Wormlike, marine forms which secrete and live in a leathery tube; they have a U-shaped digestive tract and a lophophore. (10)

16. Phylum Annelida. The segmented worms. There is a distinct head, digestive tract, celom, and—in some—nonjointed appendages. The digestive system is divided into specialized regions. (8000)

Class Polychaeta. Mostly marine worms. Each segment of their bodies has a pair of paddle-like structures (parapodia) for swimming. Some burrow in sand and mudflats; some live in calcareous tubes which they secrete; others swim freely in the ocean.

Class Oligochaeta. Fresh-water or terrestrial worms, with no parapodia and few bristles per segment.

Class Archiannelida. Primitive annelids without bristles or external segmentation.

Class Hirudinea. The leeches—flattened annelids lacking bristles and parapodia, but with suckers at anterior and posterior ends.

17. Phylum Onychophora. Rare, tropical animals, structurally intermediate between annelids and arthropods, with an annelid-like excretory system and an insect-like respiratory system. Only a few species known.

18. Phylum Arthropoda. Segmented animals with jointed appendages and a hard, chitinous skin, with a body divided into head, thorax and abdomen. (650,000)

Class Crustacea. Lobsters, crabs, barnacles, water fleas, and sowbugs. Animals that are usually aquatic, have two pairs of antennae, and respire by means of gills.

Class Chilopoda. The centipedes. Each body segment, except the head and tail, has a pair of legs.

Class Diplopoda. The millipedes. Each external segment (really two segments fused) bears two pairs of legs.

Class Arachnoidea. Spiders, scorpions, ticks, mites and king crabs. Adults have no antennae; the first pair of appendages ends in pincers,

the second pair is used as jaws, and the last four pairs are used for walking.

Class Insecta. The largest group of animals, mostly terrestrial. The body is divided into a distinct head, with four pairs of appendages; the thorax has three pairs of legs and usually two pairs of wings; the abdomen has no appendages. Respiration by means of tracheae. There are about twenty-four different orders of insects, of which the following are common:

Order Orthoptera. Grasshoppers and cockroaches.
Order Isoptera. Termites.
Order Odonata. Dragonflies and damsel flies.
Order Anopleura. Lice.
Order Hemiptera. Water boatmen, bedbugs and back-swimmers.
Order Homoptera. Cicadas, aphids and scale insects.
Order Coleoptera. Beetles, weevils and fireflies.
Order Lepidoptera. Butterflies and moths.
Order Diptera. Flies, mosquitoes and gnats.
Order Hymenoptera. Ants, wasps, bees and gallflies.

19. Phylum Mollusca. Unsegmented, soft-bodied animals, usually covered by a shell, and with a ventral, muscular foot. Respiration is by means of gills, protected by a fold of the body wall—the mantle. (80,000)

Class Amphineura. Chitons, marine forms with a shell composed of eight plates.

Class Gastropoda. Snails, slugs, whelks, abalones; asymmetrical animals with a single spiral shell, or no shell.

Class Pelecypoda. Clams, mussels, oysters, scallops. These lack a head and have a hatchet-shaped foot for burrowing. The shell consists of two plates or valves (the animals are called "bivalves"), one on each side of the body.

Class Cephalopoda. Squids, cuttlefish, octopuses. Marine animals having a well-developed "head-foot," with eight or ten tentacles, and well-developed eyes and nervous system.

20. Phylum Echinodermata. Marine animals which are radially symmetrical as adults, bilaterally symmetrical as larvae. The skin contains calcareous, spine-bearing plates. The animals have a unique water vascular system of canals, and tube feet for locomotion. Respiration is by skin gills or by outpockетings of the digestive tract. (6000)

Class Asteroidea. The starfishes. The body is a central disc with broad arms (usually five) not sharply marked off from the disc.

Class Ophiuroidea. The brittle stars and serpent stars. The body is a central disc with narrow arms sharply marked off.

Class Echinoidea. The sea urchins and sand dollars. Spherical or flattened oval animals with many long spines.

Class Holothuroidea. Sea cucumbers. Long, ovoid, soft-bodied echinoderms, usually with a ring of tentacles around the mouth.

Class Crinoidea. Sea lilies and feather stars. The body is cup-shaped and attached by a stalk to the substrate. Most of these are known only as fossils; only a few survive.

21. Phylum Chordata. Bilaterally symmetrical animals with a notochord, gill clefts in pharynx, and a dorsal, hollow neural tube. (70,000)

Subphylum Hemichorda. The acorn worms. Marine, wormlike forms resembling larval echinoderms during development.

Subphylum Urochorda. The tunicates or sea squirts. The adults are saclike, attached animals, which often form colonies, but the larval forms are free-swimming and have a notochord in the tail region.

Subphylum Cephalochorda. Amphioxus. Marine animals with a segmented, elongated, fishlike body. They burrow in the sand and take in food by the beating of cilia on the anterior end. They have a notochord extending from the tip of the head to the tip of the tail.

Subphylum Vertebrata. Animals having a definite head, a backbone of vertebrae, a well-developed brain, and, usually, two pairs of limbs. They have a ventrally located heart, and a pair of well-developed eyes.

Class Agnatha. Lampreys, hagfishes and fossil ostracoderms. Vertebrates without jaws or paired fins.

Class Placodermii. The spiny-skinned sharks. The earliest fishes with jaws, known only from fossils.

Class Chondrichthyes. Sharks, rays, skates and chimaeras. Fishes with a cartilagenous skeleton and scales of dentine and enamel imbedded in the skin.

Class Osteichthyes. The bony fishes. The sturgeon, bowfin, salmon and lungfishes.

Class Amphibia. Frogs, toads, salamanders and the extinct forms, stegocephalians. As larvae these forms breathe by gills; as adults they breath by lungs. There are two pairs of five-toed limbs; the skin is usually scaleless.

Class Reptilia. Lizards, snakes, turtles, crocodiles, the extinct dinosaurs and other forms. The body is covered with scales derived from the epidermis of the skin. The animals breathe by means of lungs and have a three-chambered heart.

Class Aves. The birds. Warm-blooded animals whose skin is covered with feathers. Present-day birds are toothless, but the primitive ones had reptilian teeth. The forelimbs are modified as wings.

Class Mammalia. Warm-blooded animals whose skin is covered with hair. The females have mammary glands which secrete milk for the nourishment of the young.

Subclass Monotremata. The monotremes, primitive forms that lay eggs. Most of them are extinct; only two species survive, the duckbilled platypus and the spiny anteater.

Subclass Marsupialia. The pouched mammals. The young are born alive, but in a very undeveloped state. They complete development in a pouch on the mother's abdomen. The subclass includes opossums, and a variety of forms found only in Australia: kangaroos, wallabies, koala bears, wombats, and so on.

Subclass Placentalia. The placental mammals. The young develop within the uterus of the mother, obtaining nourishment via the placenta.

Order Insectivora. Primitive, insect-eating mammals; moles and shrews.

Order Chiroptera. Bats.
Order Carnivora. Dogs, cats, bears, sea lions and seals.
Order Rodentia. Rats, squirrels, beavers and porcupines.
Order Lagomorpha. Rabbits and hares.
Order Primates. Monkeys, apes and man.
Order Artiodactyla. Even-toed ungulates—cattle, deer, camels and hippopotamuses.
Order Perissodactyla. Odd-toed ungulates—horses, zebras and rhinoceroses.
Order Edentata. Armadillos, sloths and anteaters.
Order Proboscidea. Elephants.
Order Cetacea. Whales.
Order Sirenia. Sea cows—large, plant-eating aquatic mammals.

INDEX

The index serves as a glossary as well; the page in the text where the definition of a term is given is indicated in **bold** type.

Abortion, 358
Absorption, **190**
  of food, 201
Abyssal region, 553
Acanthocephala, 559
Acetabularia, 35, 36
Acetylcholine, 270
Acid, **13**
Acidosis, **183**
Acorn worm, 118
Acquired characteristics, inheritance of, 469
Acromegaly, **320**
Actin, 260
Actinomyces, 397
Action currents, **152**
Adaptation(s), 31, **547–555**
  color, 550
  physiological, 548, 550
  structural, 548
Adaptive radiation, **548**
Addison's disease, 318
Adenosine triphosphate, **260**
Adrenal cortex, 317
  glands, 317
  medulla, 317
Adrenalin, 317
Adrenocorticotropic hormone, 323
Aerobic bacteria, 387
Afterbirth, 357
Agnatha, 121
Ainus, 544
Air, alveolar, 180
  composition of, 180
  quantity respired, 179
  sacs, 176, 188, 189
Alcaptonuria, **450**
Algae, 60, 61, 557
Alkali, **14**
Allantois, 353, 354, 355
Alleles, **426**
  multiple, 441
Allelomorphs, 426
Allergy, **403**
All-or-None Law, **145**, 258, 267
Alpha tocopherol, 226
  waves, **277**
Alpine race, 542
Alternation of generations, 99
Altitude sickness, 180
Alveolar air, 180
Alveoli, 176
Ameba, 168, 211, 287
Amebic dysentery, 407
Ameboid motion, 93
American Indians, 544
Amino acids, **26**, 27
    essential, 28, 217
Amitosis, 415
Amnion, **353**, 371
Amniotic cavity, 354
Amoeba proteus, 93
Amphibia, 121
Amphioxus, 120
Ampulla, 116
Anabolism, **29**, 214
Anaerobic bacteria, 387
Analogous structures, **90**
Analyses of foods, 234
Anaphase, 417, 418
Anemia, 129, **134**
  pernicious, 135, 231
Anesthetics, 291, 292
Angiosperms, 71, 75
Animal(s), blood circulation in, 167
  classification, basis for, 92
  digestive systems in, 211
  excretory devices in, 245
  kingdom, 90–122
    survey of, 558
  lower, hormones in, 329
    muscles in, 263
    nervous systems in, 287
  organization. See *Organization*.
  pole, 360
  reproduction, 344
  respiratory devices in, 188
  tissues, 38
Annelida, 106, 560
Annuals, 82
Anteater, spiny, 503
Anthropoidea, 520
Anti-insulin hormone, 323
Antibiotics, **397**
Antibodies, 133, 401
Antigen, 133
Antigen-antibody reactions, 139, **401**
Antiprothrombin, 137
Antitoxin, 401

Aorta, 143
Aphasia, **277**
Apc-men, fossil, 528
Appalachian Revolution, 494
Appendicitis, 205
Appendicular skeleton, 252
Appendix, 203
Aqueous humor, 297
Arachnida, 110
Arc, reflex, 281
Archaeopteryx, 476, 501
Archenteron, **363**
Archeology, **537**
Archeozoic Era, 487
Archiannelida, 108
Archosaurs, **495**
Arctic-Alpine region, 552
Armenoid race, 542
Arterial cone, 374
  duct, **156**
Arteries, 143
  hardening of, 164, 165
  umbilical, 155
Arthropoda, 109, 560
Artifacts, 537
Artificial respiration, 184
Ascaris, 104
Ascomycetes, 63
Ascorbic acid, 225
Asphyxia, **183**
Association areas, 277
Astigmatism, **299**
Athlete's foot, 395, 407
Atom, 11
Auditory canal, 301
Augmentation, 240, **242**
Auricle, 145, 374
Auriculoventricular node, 148
Australian region, 518
Australoids, 544
Autocatalysis, **416**
Autonomic nervous system, 284
Autotrophic plants, **51**
Auxin, **329**
Aves, 121
Avicularia, **106**
Avidin, 230
Axial skeleton, 252
Axon, 43, 265

Bacilli, 388
Backbone, 252
Bacteria, 385
  in industrial processes, 387
  metabolism of, 390
  reproduction of, 390
  types of, 387
Bacteriophages, 390, **392**
Basal metabolic rate, **215**
Basidia, 63
Basidiomycetes, 63
Basilar membrane, 303
Basophils, 132
Bats, 290
Belly of muscle, 256
Beriberi, 229
Bernard, Claude, 218
Bicuspid valve, 146
Biennials, 82
Bile, 200
  pigments, 130, 201
  salts, 200
Biochemical genetics, 450
Biogeography, 517
Biogeographic regions, 517
Biological interactions, 547
Biotin, 222, 230
Birth, 356
  changes at, 380
Blade of leaf, 86
Bladder, urinary, 240
Blastocoele, 362
Blastopore, 363
Blastula, 362
Blended inheritance, **439**
Blind spot, 298
Blindness, night, 224
Blood, 125–142
  amount of, 125
  banks, 142
  carbon dioxide transportation, 182
  cavity, 112
  cells, red. See *Erythrocytes.*
    white. See *Leukocytes.*
  circulation in animals, 167
  clotting, 136
  diseases, 134
  flow in veins, 158
  formed elements, 125, 127
  functions, 125
  groups, human, 140
    inheritance of, 441
  oxygen transportation, 181
  plasma. See *Plasma.*
  platelets, 125, 136
  pressure, 160
    capillary exchange and, 162
  proteins, 510, 511
  rate of flow, 156
  routes around the body, 153
  tests, medico-legal, 138
    in paternity, 442
  vessels, 143
    disorders of, 164
Body defenses against disease, 400
  form, development of, 369
  plan, 47
  planes, 48
  stalk, 365
  symmetry, 47
Bone(s), 41

Bone(s), breast, 252
carpal, 252
marrow, 129
metacarpal, 253
metatarsal, 253
tarsal, 253
Bowman's capsule, 240
Brachiopoda, 106, 560
Brachycephalic skull, **541**
Brain, 272
tumor, 277
waves, 277
Breast bone, 252
Breathing, control of, 184
mechanics of, 178
Bronchi, 176
Bryophytes, 66, 557
Bryozoa, 105, 560
Budding, 334
Buds, axillary, 85
lateral, 85
terminal, 85
Bushmen, 543

Calciferol, 224
Calcium, 315
Calorie, **214**
Cambium, 82, 84
Cambrian Period, 487
Cancer, 38, 167
Canine teeth, 193
Cap, root, 79
Capillaries, 143
exchange of materials in, 162
number, 144
Capsular filtrate, 240
Carbohydrate(s), **23**, 216
metabolism, 218
in protoplasm, 23
Carbon cycle, 386
dioxide transportation by blood, 182
Carbonic anhydrase, 183
Carboniferous Period, 491
Carotene, **87**, 223
Carpal bones, 252
Cartilage, 41, 251
Cast fossils, 482
Catabolism, **29**, 214
Catalysis, 29
Catalyst, **29**, 30
Catarrhine monkeys, 521
Catastrophism, **468**
Cathepsin, 207
Cecum, 510
Cell(s), 34–38
body, 42
epithelial, 39
flame, 102, 245
interstitial, 323, 348
palisade, 87
Cell(s), plate, 419
wall, 35
Celom, **92**, 106, 107, 366
Cement of teeth, 192
Cenozoic Era, 501
Center of origin, **517**
Centipedes, 110
Central nervous system, 271
Centriole, **37**, 418
Centrum, 252
Cephalic index, **541**
Cephalochordata, 119, 562
Cephalopoda, 115
Cerebellum, 274
Cerebral cortex, 275
hemispheres, 275
Cerebrospinal fluid, 272
Cerebrum, 274
Cervix, 350
Cestoda, 102
Chaetognatha, 559
Chimpanzees, 522
Chiton, 113
Chlorophyceae, 62
Chloroplast, 37, 54
Cholecystokinin, 328
Choline, 231
Cholinesterase, 270
Chondrichthyes, 121
Chordata, 118, 561
Chorea, Huntingdon's, 457
Chorion, 353, 354, 355
Choroid coat, 296
Chromatin, **35**, 36, 415
Chromomeres, 415
Chromonema, 415
Chromoplast, 37
Chromosome(s), 36, 415
homologous, **420**, 422
mutations, 476
number, 415
sex, 443
structure, 415
Chyme, 198
Cilia, 95
Ciliary body, 297
ligament, 297
Ciliata, 95
Circulation, blood, in animals, 167
fetal, 154
plant, 57, 171
Circulatory system, 143–172
Clavicle, 252
Cleavage, 361
in frog and chick eggs, 363
in human egg, 364
Clitoris, 351
Clotting of blood, 136
Club moss, 70
Coeci, 388
Cochlea, 302, 303

Cochlear canal, 303
Coelenterata, 97, 168, 559
Coenzyme, **229**, 230
Collenchyma, **44**
Colloid, **15**
Colon, 203
Colony, social, 112
Color adaptations, 550
  of eyes, 456
  of hair, 455
  of skin, 250
Coloration, protective, 550
  warning, 550
Commensalism, **102**
Compound(s), **13**
  in protoplasm, 22, 23
Condiments in diet, 221
Conditioned reflex, **282**, 283
Conduction, 265
Condylarths, 506
Cones, 298
Conifer, 73
Connector neurons, 265
Conservation of Matter, Law of, **14**
Constipation, 204
Contraception, 461
Contractile vacuole, 37, 94, 95, 245
Contraction, muscular, 258, 262
    chemistry of, 260
  period, 259
Convergent evolution, 115, **548**
Coordination in plants, 67
Copulation, 351
Corals, 99
Cork cambium, 84
Cornea, 296
Corona radiata, **351**
Corpus luteum, **325**
Corpuscles, red. See *Erythrocytes*.
Cortex of root, 80
Cortin, 318
Cowper's glands, 348
Cranial index, **541**
  nerves, 280, 281
Cranium, 252
Creatine, 224
Creodonts, 505
Cretaceous Period, 495
Cretin, **311**, 312
Cretinism, 311
Cro-Magnon man, 535
Crocodiles, 500
Crop, 107
Cross, dihybrid, 434
  monohybrid, 427, 434
  test, 429
Crossing over, **445**
Crown of teeth, 192
Crustacea, 109
Ctenophora, 100, 559
Cultural evolution, 537
Curare, 256
Cutin, 67
Cyanophyceae, 61
Cycads, 73, 74
Cytochrome, **131**, 221
Cytoplasm, **37**

Dandruff, 250
Darwin, Charles, 469 ff.
Dead space, **179**
Deafness, 305
Deamination, **28**, 219
Decay, 386
Defecation, 203, 204, 238
Dementia praecox, **279**, 457
Dendrite, 43, 265
Dentrifying bacteria, 387
Dentine, 192
Dermis, 249
Detoxification, **217**, 218
Development, control of, 378
Devonian Period, 489
de Vries, Hugo, 474
Diabetes, 243, 315
  insipidus, 244, 320
Dialysis, **18**
Diaphragm, 177
Diarrhea, 204
Diastase, 207
Diastole, **149**
Dicotyledons, 76
Diet, 233
  components of, 220
  condiments in, 221
  roughage in, 221
Diffusion, **16**
Digestion, 190
  chemistry of, 205
  enzymes important in, 206
  plant, 57
Digestive glands, stimulation of, 209
  system, 190–213
    in animals, 211
  tract, development of, 375
    disorders of, 205
    microscopic anatomy, 194
Digitigrade, **254**
Dihybrid cross, 434
Dinaric race, 542
Dinosaurs, 500
Diploid number, **420**
Disease, body defenses against, 400
  functional, 308
  germ theory of, 397
  infectious, 399
Dolichocephalic skull, **541**
Dominance, incomplete, 430
Dominant gene, **427**
Dryopithecus, 528
Duckbilled platypus, 503

Duct, arterial, 156
Ductus arteriosus, 156
Duodenum, 198
Dynamic equilibrium, 130
Dysentery, amebic, 407

Ear, 301
  drum, 301
  efficiency of, 304
  evolution of, 305
Earthworm, 106, 169, 212, 287
Echinodermata, 115, 561
Ecologic niche, **54**
Ecology, 547
Ectoderm, 363, 377
Ectoplasm, 37
Edema, **126**, 167, 244, 456
Effector, **265**
Egg(s), 43, 333
  types of, 360, 361
Electric organ, 264
Electrocardiograph, **152**
Electroencephalograph, **277**
Electrolyte, **14**
Electron, **11**
  microscope, 385
Element(s), **12**
  in protoplasm, 21
Embolus, **138**
Embryo, 362, 369
  development of, 360–382
  nutrition of, 353
Embryonic membranes, 353
Emotions, 284
Emulsion, **15**
Enamel, 192
Endocrine glands, interrelationships, 329
  system, 308–330
Endodermis of root, 80
Endolymph, **303**
Endoplasm, 37
Endoskeleton, 251
Endosperm, **343**
Endothelium, 145
Endotoxins, 399
Energy, **15**
  requirements, 215
Enterokinase, 208
Entoderm, 363, 377
Environment, effect on genes, 451
Environmental resistance, **548**
Enzymes, **29**, 30, 205
  important in digestion, 206
  respiratory, 131
Eoanthropus dawsoni, 532
Eocene Epoch, 502
Eosinophils, 132
Epidermis, 67, 249
  bullosa, 456
  of leaf, 86
Epidermis of root, 80
Epididymis, 348
Epigenesis, **378**
Epiglottis, 175
Epilepsy, 277, 458
Epinephrine, 317
Epithelium, 39
  germinal, 325
  pavement, 39
Equilibrium, 306
  dynamic, 130
Eras, geological, 487
Erepsin, 208
Erythrocyte(s), 125, 127
  count, 128
  life history, 129
Eskimos, 544
Esophagus, 196
Essential amino acids, **28**, 217
Estrogen, 325
Estrus cycle, **326**
Ethiopian region, 518
Eugenics, **460**
Eunuch, 323
Eurypterid, 489
Eustachian tubes, 195, 301
Evolution, 467–555
  anatomic evidence for, 509
  convergent, 115, 548
  cultural, 537
  of ear, 305
  embryologic evidence for, 512
  evidence from biochemistry, 510
    from geographic distribution, 516
    from physiology, 510
  fossil evidence for, 482–508
  genetic evidence for, 515
  of heart, 169
  human, 520–546
  inorganic, 467
  living evidence for, 509–519
  of lungs, 186
  of man, 535
  organic, **467**
  outcome of, 547–555
  principles of, 480, 481
  reptilian, 495
  sexual, 336
  straight-line, 477
Excretion, 238
  in plants, 59, 247
Excretory devices in animals, 245
  system, 238–247
Exophthalmic goiter, 312
Exophthalmos, 312
Exoskeleton, 251
Exotoxins, 399
Expressivity, 447, **448**
Extensor muscle, 257
Eye color, 456
  human, 296

Eye, mosaic, 296
muscles, 298
spots, 295

Facial index, 541
Facilitation, **283**
Fallopian tubes, 349
Far sightedness, 299
Fat(s), 23, **25**, 26, 216
metabolism, 219
in protoplasm, 25
Fat-metabolism hormone, 323
Fatigue, **262**
Feces, 204
Feeble-mindedness, 459
Femur, 253
Fermentation, **390**
Fern, 69
life cycle, 341
Fertilization, **345**, 351
Fetal circulation, 154
Fibrin, 136
Fibula, 253
Filaria, 104
Filtrate, capsular, 240
Filtration, **240**, 241
Fingernails, 250
Fingerprints, 249
Fission, **334**
Fissure of Rolando, 276
Flagella, 96
Flagellata, 96
Flame cell, 102, 245
Flatworms, 100
Flexor muscle, **257**
Flower, 341
Fluid, tissue, 144
Folic acid, 230
Follicle-stimulating hormone, 322
Food, absorption of, 201
analyses, 234
storage in plants, 89
vacuole, 37, 94, 99, 211
Foramen ovale, 155, 301, 375
Foraminifera, 94
Forest, rain, tropical, 552
Fossil, **482**
ape men, 528
members of genus Homo, 532
primates, 527
Fovea, 298
Fragmentation, 334
Frontal section, 48
Fructose, 24
Fruit, 344
scars, 86
Fuels, body, 217
Functional diseases, 308
Fundus of stomach, 197
Fungi, 60, 63, 394, 556
imperfect, 65

Galactose, 24
Gallbladder, 200
Gallstones, 201
Galley Hill man, 534
Gametes, **333**
law of purity of, 429
Gametophyte, 338
Ganglia, **165**, 280
Gas exchange in lungs, 180
Gastric juice, 206
Gastrin, 209
Gastrocnemius muscle, 258
Gastrocolic reflex, 203
Gastropoda, 114
Gastrotricha, 105, 560
Gastrovascular cavity, 97, 98
Gastrula, 362
Gastrulation, 362
in frog and chick eggs, 363
in human egg, 364
Gel, **16**
Gene(s), 36, 415, **426**
complementary, **436**
dominant, 427
effect of environment on, 451
hybrid, 428
interactions of, 436
lethal, **441**
mutations, 476
recessive, 427
supplementary, **437**
Generation(s), alternation of, 99
filial, 428
parental, 428
spontaneous, 31
Genetics, 414, 434–452
biochemical, 450
Genotype(s), **428**
deducing, 431
Genus, **59**
Geologic time table, 484, 486
Geological eras, 487
revolutions, 486
Geotropism, **57**
Germ layer, contributions of, 377
theory of disease, 397
Germinal epithelium, 325
Gestation period, 373
Gibbons, 521
Gigantopithecus, 532
Gill(s), 189
slits, 375
Ginkgo, 73, 74
Gizzard, 107
Glaciation, 507
Gland(s), adrenal, 317
Cowper's, 348
digestive, 209
endocrine, 329
mammary, 249
parathyroid, 313

Gland(s), parotid, 194
pineal, 329
pituitary, 318
prostate, 348
salivary, 193
sublingual, 194
submaxillary, 194
thyroid, 310
Glomerulus, 240
Glucose, 13, 23, 24, 218
Glycogen, 25, 218
Gnetales, 74, 75
Goiter, 220, 221, **311**
exophthalmic, **312**
Goldschmidt, R., 475
Golgi bodies, **37**
Gonadotropic hormones, 320
Gorillas, 522
Gout, 512
Gram, 9
Grana, **54**
Gristle, 41
Ground pines, 70
Growth, 30
hormone, 320
Guinea worm, 104
Gymnosperms, 71, 72

Habit, 283
Habitat, **547**
Hair, 250
color, 455
"peppercorn," 543
root, 79
Haploid number, **420**
Harmonics, 304
Hearing, theory of, 303
Heart, 145
"attack," 164
beat, 147
adaptation to body activity, 153
cycle, 149
disorders of, 164
electrical changes in, 151
evolution of, 169
formation of, 373
regulation of, 153
sounds, 151
Heartwood, 83
Heat regulation, 248, 249
Heidelberg man, 533
Hemichorda, 562
Hemocyanin, 131
Hemocytometer, 128
Hemoglobin, 26, 104, 128, 181
Hemophilia, 138
Hepatic portal system, 154
Heredity, 413
physical basis, 413–433
Hermaphroditism, **344**
Heterotrophic plants, 52
Heterozygous genes, 428
"High energy phosphate bonds," **261**
Hirudinea, 108
Holarctic region, 518
Holozoic nutrition, **52**
Hominidae, 520
Homo heidelbergensis, 533
neanderthalensis, 533
rhodesiensis, 534
sapiens, 534
soloensis, 533, 534
Homologous structures, **90**
Homology, 509
Homozygous genes, 428
Hookworm, 104
Hormone(s), **209**, 308
adrenocorticotropic, 323
anti-insulin, 323
fat-metabolism, 323
follicle-stimulating, 322
gonadotropic, 320
growth, 320
lactogenic, 322
in lower animals, 329
luteinizing, 322
pituitary, 323
in plants, 329
thyrotropic, 323
Horsetails, 69
Hottentots, 543
Hudsonian-Canadian region, 552
Humerus, 252
Hunger, 293
Huntington's chorea, 457
Hyaluronic acid, 351
Hyaluronidase, 351
Hybrid genes, 428
vigor, **448**
Hybridization, 479
Hydra, 97, 211, 287
Hymen, 351
Hyperthyroidism, **312**
Hypertonic fluid, **20**
Hypertrichosis, **456**
Hypothyroidism, **312**
Hypotonic fluid, **20**

Ichthyosaurs, 501
Ichthyosis, **456**
Idiocy, amaurotic, juvenile, 457
Idiots, 459
Imbeciles, 459
Immune carrier, 404
Immunity, acquired, 401
natural, 402
Implantation, 352, 353
Impulse(s), nerve, 266, 291. See also *Nerve*
transmission in plants, 288
Inbreeding, 448
Incisor teeth, 193

Incomplete dominance, 430
Index, cephalic, 541
  cranial, 541
  facial, 541
  nasal, 541
Indians, American, 544
Indigestion, 205
Indonesians, 544
Infantile paralysis, 405
Inferior vena cava, 146
Inflammation, 133, 401
Ingestion, 190
Inguinal canal, 347
Inheritance, blended, 439
  of blood groups, 441
  of intelligence, 458
  in man, 453–463
  of mental disorders, 457
  of mental traits, 457
  of physical traits, 454
  of skin color, 439, 440
  of special abilities, 460
Inhibition, **271**
Inoculation, **401**
Inositol, 230, 232
Insanity, 278
  manic-depressive, 458
Insects, 110, 169
  parasitic, 395
Insertion of muscle, 256
Instincts, **112**
Insulin, 316
Integration, **265**
Integument, 248
Integumentary system, 248–250
Intelligence, classification of, 459
  inheritance of, 458
  quotient, 459
Interactions, biological, 547
  gene, 436
Internode, 85
Intersex, **443**
Interstitial cells, 323, 348
Intestinal juice, 208
  movements, 199
Intestine, large, 203, 204
  small, 198
Iodine, 220, 221
  radioactive, 313
Ion, **13**
Iris, 296
Irritability, **31**
Ischial callosities, 521
Islet cells of pancreas, 315
Isolation, **471**, 472
  ecological, 472
  genetic, 472
  geographic, 471, 472
Isolecithal egg, **360**
Isotonic fluid, **20**
Isotope, **12**

Java ape man, 530
Jellyfish, 99
Joints, 253
Jurassic Period, 495
Juvenile amaurotic idiocy, 457

Kangaroo, 505
Ketone bodies, **316**
Kidney, 239
  development of, 375
  diseases of, 244
  pelvis, 239
  regulatory function of, 243
  stones, 245
  threshold, **243**
Kinesthesis, **292**, 293
Knee cap, 253
Koch's postulates, 398

Labia, 350, 351
Labyrinth, 302
Lactase, 208
Lactose, 24
Lactogenic hormone, 322
Lamarck, Jean Baptiste de, 469
Larynx, 175
Latent period, 259
Latex, 127
Law, All-or-None, 145, 258, 267
  of Conservation of Matter, 14
  of Independent Segregation, 343
  of Segregation, 429
Learning, 283
Leaf epidermis, 86
  functions, 86
  scars, 86
Leaves, 66
Leeches, 108
Lemurs, 520
Lens, 296
Lenticel, 84
Leukemia, **135**
Leukocyte(s), 125, 131
  count, differential, 132
  life history, 134
Leukoplast, 37
Lichens, 65
Life cycle(s), 338
    of fern, 341
    of mosses, 339
    of seed plant, 341
  zones, marine, 552
    terrestrial, 552
Ligament, 40, 251
  ciliary, 297
Lignin, 46, 254
Linkage, **445**
  specific, 447
  group, **447**

Lipase, 207
Liver, 200, 217, 218
  fluke, 102, 103
Liverworts, 68
Living things, characteristics of, 28
Lizards, 495
Locomotion, types of, 254
Lophophore, 105, 106
Lungs, 176, 177
  evolution of, 186
  gas exchange in, 180
Lungfish, 188
Luteinizing hormone, 322
Lymph flow, 166
  nodes, 165
  system, 165
    functions, 166
Lymphocytes, 132

Macromutation, 474
Malaria, 96, 335
Malformations, 380
Malpighian tubules, 246
Maltase, 208
Maltose, 24
Mammalia, 121
Mammals, Age of, 501
Mammary glands, 249
Man, Age of, 506
  Cro-Magnon, 535
  Galley Hill, 534
  Heidelberg, 533
  modern, 534
  Neanderthal, 533
  other primates and, 520
  Peking, 530
  Piltdown, 532
  races of, 540
  Rhodesian, 534
  Solo, 533
Manic-depressive insanity, 458
Mantle, 113
Marrow, bone, red, 129
  cavity, 41
  yellow, 129
Marsupials, 505
Matter, Conservation of, 14
  structure of, 10
Mechanism, 28
Mediterranean race, 541
Medulla, 273
Medullary rays, 82
Meganthropus, 530
Meiosis, **420**
Melanesian race, 543
Melanin, 318
Membrane, 18
  basilar, 303
  elastic, internal, 143
  embryonic, 353
Membrane, nuclear, 35
  plasma, 34, 35
  roof, 303
  theory, 268
Memory, 283
Mendel, Gregor, 414
Mendel's First Law, 429
  Second Law, 434
Meninges, 272
Menstrual cycle, **326**
Menstruation, 221, **326**
Mental disorders, inheritance of, 457
  traits, inheritance of, 457
Meristem, **44**
Mesocephalic skull, **541**
Mesoderm, 365, 377
Mesolithic culture, 539
Mesonephros, **377**
Mesophyll, 87
Mesozoic Era, 495
Metabolism, **29,** 214–237
  bacterial, 390
  carbohydrate, 218
  fat, 219
  protein, 219
Metacarpal bones, 253
Metamorphosis, **313,** 346
Metanephros, **377**
Metaphase, 417, 418
Metatarsal bones, 253
Metazoa, 92
Meter, 9
Metric system, 9
    units and English equivalents, 10
Micro-organisms as cause of disease, 399
  infectious diseases and, 385–410
  spread of, 404
Microscope, electron, 385
Midbrain, 274
Midget, 320
Milk, 358
Millipedes, 110
Milroy's disease, 456
Mimicry, **551**
Mimosa pudica, 288, 289
Mineral(s) in diet, 220
  salts in protoplasm, 22
Miocene Epoch, 502
Miscarriage, 358
Misreference, **292**
Mississippian Period, 491
Mitochondria, 37
Mitogenic rays, **420**
Mitosis, 361, **415**
  control of, 419
Modifications, **471**
Modifying factors, 441
Molar teeth, 193
Mold fossils, 482
Molecule(s), **13**
  motion of, 16

Mollusca, 113, 561
Mongolian fold, 456
  spot, 456
Mongoloid race, 543
Monkeys, 521
Monocotyledons, 76
Monocytes, 132
Monohybrid cross, 427, 434
Monotremes, 503
Mons Veneris, 350
Moods, 284
Morons, 459
Mosaic eye, 296
Mosasaurs, 495
Mosses, 66
  club, 70
  life cycle, 339
  Spanish, 66
Motor neurons, 265
Mousterian culture, 539
Mouth cavity, 190
Multiple alleles, **441**
  factors, **439**
Muscle(s), belly of, 265
  cardiac, 256, 263
  contraction, 258
    chemistry of, 260
    contraction period, 259
    latent period, 259
    nature of, 262
    recovery period, 259
    relaxation period, 259
  extensor, 257
  eye, 298
  flexor, 257
  gastrocnemius, 258
  insertion of, 256
  in lower animals, 263
  origin of, 256
  skeletal, 256
  smooth, 256, 263
  sphincter, 196
  tissues, 42
  tonus, 260
Muscular system, 256–264
Mutation(s), 471, 474
  causes of, 477
  chromosome, 476
  frequency of, 476
  gene, 476
  theory of de Vries, 474
  types of, 476
Mutualism, **102**, 208
Myelin sheath, 265, 266
Myosin, 260
Myxedema, **310**
Myxomycetes, 63

Nares, 174
Nasal chamber, 174
  index, 541
Natural Selection, changes in, 471
    Theory of, 470
Nausea, 294
Navel, 357
Neanderthal man, 533
Nearctic region, 518
Near-sightedness, 299
Negritos, 543
Negroid race, 542
Negroids, Oceanic, 543
Nematocysts, **99**
Nematoda, 104, 559
Nematomorpha, 560
Nemertea, 103, 559
Neolithic culture, 540
Neotropical region, 518
Nephridium, **107**, 246
Nephritis, 244
Nereis, 108
Nerve(s) center, 265, 273
  cranial, 280, 281
  impulse, 266, 291
    membrane theory, 268
    nature of, 266
  net, **287**
  parasympathetic, 284
  spinal, 281
  sympathetic, 284
  trunks, 265
Nervous system, 265–289
    autonomic, 284
    central, 271
    development of, 368
    in lower animals, 287
    parasympathetic, 285, 286
    parts of, 271
    peripheral, 271, 279
    sympathetic, 285, 286
Neural arch, 252
  crest, **369**
  groove, 368
  plate, 368
Neurilemma sheath, 265, 266
Neuron, 42
  types of, 265
Neuroses, 278, **279**
Neurospora, 222, 450
Neutron, **11**
Neutrophils, 132
Niacin, 229
Nicotinic acid, 229
Night blindness, 224
Nitrate bacteria, 387
Nitrogen cycle, 387
Nitrogen-fixing bacteria, 387
Nodal tissue, 148
Node(s), 85
  auriculoventricular, 148
  lymph, 165
  sino-auricular, 148
Nonelectrolytes, 14

Nordic race, 542
Notochord, 119, 120, 367
Nuclear membrane, 35
Nucleolus, 36, 37
Nucleoplasm, 35
Nucleoplasmic ratio, **419**
Nucleoproteins, 450
Nucleus, 35
Nutrition, 214–237
  of embryo, 353
  of infant, 358
  plant, 51

Octopus, 115
Oedogonium, 337
Oligocene Epoch, 502
Oligochaeta, 108
Onychophora, 559
Oöcytes, 425
Oögenesis, 424
Oögonia, 424
Oötid, 425
Optic lobes, 274
Orang-utan, 521
Ordovician Period, 488
Organ of Corti, 303
  systems, 47
Organic compounds, 23
Organization, animal, cellular level, 96
    organ level, 100
    organ system level, 103
    protoplasmic level, 93
    tissue level, 97
  specific, 33
Organizers, **378**, 379
Oriental region, 518
Origin of muscle, 256
Origin of Species, 470
    background for, 469
Ornithischia, 500
Orthogenesis, **478**
Osmosis, **19**
Osmotic pressure, **19**
Osteichthyes, 121
Ostracoderm, **489**
Outbreeding, 448
Oval window, **155**, **301**, 375
Ovaries, 325, 349
Overtones, 304
Oviduct, 325, 349
Ovulation, **325**, 327
Oxygen debt, **262**
  transportation, 128
    by blood, 181
Oxygen-carrying devices, 130

Pacemaker, **148**
Palearctic region, 518
Paleocene Epoch, 502
Paleolithic culture, Lower, 537
    Middle, 539
    Upper, 539
Paleontology, 482
Paleozoic Era, 487
Palisade cells, 87
Pancreas, 201, 207, 208
  islet cells, 315
Pancreatic juice, 207
Pantothenic acid, 230
Para-aminobenzoic acid, 230, 232
Paralysis agitans, 457
  infantile, 405
Paramecium, 95, 168, 287, 338
Paranoia, **279**
Paranthropus, 528
Parapithecus, 527
Parasitism, **52**, 102
Parasympathetic nervous system, 285, 286
Parathyrin, 314
Parathyroid glands, 313
Parenchyma, 44
Parotid glands, 194
Parthenogenesis, **344**
Parturition, **356**
Pasteurization, 398
Patella, 253
Pavement epithelium, 39
Pavlov, Ivan Petrovich, 209, 282, 283
Pectoral girdle, 252
Pedigree, 453
Peking man, 530
Pelagic zone, 553
Pelecypoda, 114
Pellagra, 229
Pelvic girdle, 252
Pelvis, kidney, 239
Pelycosaurs, 494
Penctranee, 447, **448**
Penicillin, 63, 397
Penis, 348
Pennsylvanian Period, 491
"Peppercorn" hair, 543
Pepsin, 206
Perception of sensations, 291
Perennials, 82
Pericycle, 80
Perilymph, 303
Peripatus, 109
Peripheral nervous system, 271, 279
Peristalsis, **196**, 199, 200
Permian Period, 494
Pernicious anemia, 135, 231
Perspiration, 249
Petal, 342
Petiole, 86
Petrifaction, 482
*p*H, **14**
Phaeophyceae, 62
Phalanges, 253
Pharynx, 174, 195

Phenotype, **428**
Phenylketonuria, **457**
Phloem, 46, 171
Phoronida, 560
Phosphate bonds, high energy, 261
Phosphocreatine, 260
Photosynthesis, 51, **52**, 56
Phototropism, **57**
Phycomycetes, 63
Phylum, **60**
Physical traits, inheritance of, 454
Physicochemical background, 9–20
Phytosaurs, 500
Pigments, bile, 130, 201
Piltdown man, 532
Pineal gland, 329
Pines, ground, 70
Pistil, 342
Pith, 82
Pithecanthropus erectus, 530
Pitocin, 319
Pitressin, 319
Pituitary, 318
  gland, anterior lobe, 320
    posterior lobe, 319
  hormones, 323
Placenta, 328, 355
Placodermii, 121, 489
Planaria, 101, 102, 168, 212
Planes, body, 48
Plantigrade, **254**
Plant(s), annual, 82
  biennial, 82
  circulation in, 57, 171
  conquest of land by, 66
  coordination, 57
  digestion, 57
  economic importance, 89
  hormones, 329
  excretion, 59, 247
  food storage, 89
  kingdom, 51–77
    survey of, 557
  nutrition, 51
  perennial, 82
  respiration, 56
  sap, 80, 127
  seed, 78
  skeletal system, 254
  transmission of impulses, 288
  types of, 59
Plasma, 125
  dried, 142
  glucose, 126
  membrane, 34, 35
  proteins, 126
  salts, 126
Plastids, 37
Platelets, blood, 125, 136
Platyhelminthes, 100, 559
Platypus, duckbilled, 503
Platyrrhine monkeys, 521
Pleistocene Epoch, 506
Plesiosaurs, 501
Pleura, 177
Pliocene Epoch, 502
Pole, animal, 360
  vegetal, 360
Pollen, 343
  tube, 71, 343
Polocyte, **425**
Polychaeta, 108
Polycythemia, **135**
Polyploids, 476
Pons, 274
Porifera, 96, 559
Portuguese man-of-war, 99
Posture, 257
Potential reproductive rate, 547
Preadaptation, **473**
Preformation, **378**
Pregnancy, 328
Premolar teeth, 193
Pressure, blood. See *Blood*.
  osmotic, 19
  pulse, 161
  root, 80
Primates, 520
  fossil, 527
Primitive streak, 367
Proboscis worm, 103
Progeny selection, **430**
Progesterone, 325
Pronephros, **377**
Prophase, 417
Propliopithecus, 527
Proprioceptors, **292**
Prostate gland, 348
Protective coloration, **550**
Protein(s), 23, **26**, 216
  blood, 510, 511
  metabolism, 219
  in protoplasm, 26
Proterozoic Era, 487
Prothrombin, 137
Proton, **11**
Protoplasm, **21–33**, 34
  carbohydrates in, 23
  chemical composition, 21
  compounds in, 22, 23
  fats in, 25
  mineral salts in, 22
  physical characteristics, 21
  proteins in, 26
  salt content, 22
  water content, 22
Protozoa, 93, 559
  parasitic, 395
Pseudopods, **93**
Psychoses, **279**
Pteridophytes, 69, 558
Pterosaurs, 500

Ptyalin, 194, 206
Pulp, tooth, 192
Pulse, 158
  pressure, 161
Pupil of eye, 296
Pus, 133
Putrefaction, **390**
Pygmies, 543
Pylorus, 197
Pyridoxine, 230

Quarantine, 404
Quaternary Period, 501, 505
Quillwort, 70

Races of man, 540
    Ainus, 544
    Alpine, 542
    Armenoid, 542
    Australoids, 544
    Dinaric, 542
    Mediterranean, 541
    Melanesian, 543
    Mongoloid, 543
    Negroid, 542
    Nordic, 542
    Tasmanian, 543
    Veddoids, 544
    white, 541
Radiation, adaptive, 548
Radioactive iodine, 313
Radiolaria, 95
Radius, 252
Radula, 113
Rain forest, tropical, 552
Rays, medullary, 82
Reabsorption, 240, **242**
Reaction, antigen-antibody, 139, 401
  chemical, 14
Recapitulation, theory of, **376**, 514
Recent Epoch, 506
Receptor, 265
Recessive genes, 427
Recovery period, 259
Rectum, 203
Reflex, **281**, 282
  arc, **281**
  conditioned, 282, 283
  gastrocolic, 203
Refractory period, **263**, 267
Reinforcement, **271**
Relaxation period, 259
Renin, 244
Rennin, 207
Reproduction, 31
  animal, 344
  asexual, 333, 334
  bacterial, 390
  human, 347–359
Reproduction, methods of, 333–346
  sexual, 333, 336
    in animals, 344
Reproductive organs, female, 349
    male, 347
  rate, potential, 547
Reptiles, stem, 491
Reptilia, 121
Resistance, environmental, 548
Respiration, artificial, 184
  direct, **173**
  external, **174**
  indirect, **174**
  internal, **174**
  plant, 56
Respiratory center, 184
  devices in animals, 188
  enzymes, 131
  system, 173–189
    human, 174
Retina, 296
Revolutions, geological, 486
Rheumatic fever, 164
Rh factor, **141**
Rhizoids, 67
Rhodesian man, 534
Rhodophyceae, 62, 63
Riboflavin, 229
Rickets, 225
Rickettsia, 390, 393
Rigor mortis, 263
Rocky Mountain Revolution, 495
Rods, 298
Roof membrane, 303
Root(s), 66
  cap, 79
  cortex, 80
  endodermis, 80
  epidermis, 80
  functions, 78
  hair, 79
  pressure, 80
  tap, 81
  of teeth, 192
  stocks, 336
  types of, 81
Rotifera, 105, 560
Roughage in diet, 221
Round window, 302
Runners, 335

Saccule, 306
Sagittal section, **48**
Saliva, 206
Salivary glands, 193
Salt(s), **14**
  bile, 200
  mineral, in protoplasm, 22
Sap, plant, 80, 127
Saprophytic nutrition, **52**

Sapwood, 83
Sarcodina, 94
Saurischia, 500
Scapula, 252
Scar(s), fruit, 86
  leaf, 86
  tissue, 133
Schizophrenia, **279**
Sclera, 296
Sclerenchyma, 44
Scrotal sac, 347
Scurvy, 221, 225, 226
Sea anemones, 99
  cucumber, 115, 117, 118
  lilies, 115, 118
  squirts, 119
  stars, 115
  urchin, 115, 117
Secretin, 210, 328
Secretion, **238**
Seed, **343**
  fern, 73
  plants, life cycle, 341
    structure and function, 78–89
Segmentation, **92**
Segregation, Independent, Law of, 434
  Law of, 429
Semen, 348
Semicircular canals, 306
Semilunar valve, 146
Seminal fluid, 348
  vesicles, 348
Seminiferous tubules, 347, 348
Sensations, perception of, 291
Sense organs, 290–307
Senses, chemical, 294
  tactile, 292
Sensitive plant, 288, 289
Sensitivity, visceral, 293
Sensory neurons, 265
Sepal, 342
Serpent star, 115, 117
Serum, **127,** 136, 142, **402**
Sex cells, 333
  chromosomes, 443
  evolution of, 336
  genetic determination of, 443
Sex-influenced characters, 444
Sex-linked characters, 444
Seymouria, 491
Shallow sea zone, 553
Shock, **164**
Shrub, 82
Siamese twins, 379
Sieve tube, 47
Silurian Period, 489
Sinanthropus pekinensis, 530
Single twitch, **258**
Sino-auricular node, 148
Sinus venosus, 148, 374
Skeletal system, 250–255
Skeleton, 250
  parts of, 252
  of plants, 254
  types of, 251
Skin, 248
  color, 250
    inheritance of, 439, 440
      multiple factor, 440
  outgrowths of, 250
  parts of, 249
Skull, 252
Sleep, 277
Smell, 294, 295
Snakes, 495
Sol, **16**
Solo man, 533
Solution, **15**
Somite, 371
Sonoran region, 552
Sounds, heart, 151
Spanish moss, 66
Species, **59**
  specificity, **27**
Specific dynamic action, **217**
Sperm, 43, 333
Spermatids, 423
Spermatocytes, 423
Spermatogenesis, 422
Spermatogonia, 422
Spermatophyta, 558
Spermatophytes, 71
Sphincter muscle, 196
Sphygmomanometer, **160**
Spinal ataxia, 457
  cord, 271
  nerves, 281
Spindle fibers, 418
Spiny anteater, 503
Spiracles, 189
Spirochetes, 389
Spirogyra, 336
Sponges, 96, 287
Spontaneous generation, **31**
Sporangia, 335
Spores, 335
Sporophyte, **339**
Sporozoa, 96
Squid, 115
Stalk, body, 365
Stamen, **342**
Starfish, 115, 116
Steatopygia, **543**
Stegocephalians, 490
Stem(s), 66
  functions of, 81
  reptiles, 491
Sterility, 226
Sterilization, 461
Steroids, 318, 323
Stimuli, intensity of, 292
  localization of, 292

Stimulus-receiving process, 291
Stomach, 197
  fundus, 197
  pylorus, 197
  ulcer, 205
Stomata, 68
Stone Age culture, Middle, 537
    New, 540
Streptomycin, 397
Sublingual glands, 194
Submaxillary glands, 194
Sucrase, 208
Sugars, compound, 24
  double, 24
  relative sweetness, 24
  simple, 23
Superior vena cava, 146
Survival of the fittest, 470
Suspensions, 15
Swallowing, 190, 196
Swanscombe skull, 534
Sweat, 238
Swim bladder, 187, 188
Symbiosis, **208**
Symmetry, body, 47, 48
Sympathetic nervous system, 285, 286
Sympathin, 270
Symptoms, disease, 399
Synapse, 43, 268
  transmission across, 270
Synapsis, **420**
Syphilis, 405
Systole, **149**

Tap roots, 81
Tapeworm, 102, 103
  infections, 408
Tarsal bones, 253
Tarsius, 520
Tasmanian race, 543
Taste, 294
  buds, 294
Teeth, 192
  canine, 193
  incisor, 193
  molar, 193
  premolar, 193
Teleosts, 490
Telolecithal egg, **360**
Telophase, 417, 418
Tendon, 40, 251
  of Achilles, 258
Termite, 112, 208
Tertiary Period, 501
Test(s), blood, 138, 442
    medico-legal, 138
  cross, **429**
  Wassermann, 407
Testes, 323, 347, 348
Testosterone, 323
Tetanus, **259**
Tetany, **314**
Tetrad, **421**
Thalamus, 274
Thallophyta, 60, 557
Thallus, 60
Therapsids, 494
Thiamine, 228
Thirst, 293
Thrombin, 137
Thrombokinase, 136
Thrombus, **137**
Thymus, 329
Thyroglobulin, 310
Thyroid glands, 310
Thyrotropic hormone, 323
Thyroxine, 310
Tibia, 253
Tidal zone, 553
Tissue(s), animal, 38
  connective, 40
  culture, 38, 138
  epithelial, 38
  fluid, **144**
  fundamental, 44
  meristematic, 44
  muscle, 42
  nervous, 42
  nodal, 148
  plant, 44
  protective, 44
  reproductive, 43
  scar, 133
  vascular, 42
Tocopherol, 226
Tongue, 190
Tonus, 257, **260**
Tooth pulp, 192
Touch, 292
Toxin, **399**
Toxoid, 402
Trachea, 175
Tracheal tubes, 112, 189
Tracheids, 46
Training, effect on respiration, 186
Transfusions, blood, 139
Transitional region, 552
Translocation, **447**
Transpiration, **88**
Transport of carbon dioxide, 182, 183
  of oxygen, 181, 182
Transverse section, **48**
Tree, 82
  fern, 69
Trematoda, 102
Triassic Period, 495
Trichina worm, 104
Trichinosis, 409
Tricuspid valve, 146
Trihybrid cross, 434
Trochophore larva, 113

Tropical rain forest, 552
Tropism, **57**
Trypsin, 207
Tuatera, 495
Tubes, pollen, 71
Tumor, brain, 277
Tunicates, 119
Turtles, 495
Twinning, 379
Twins, 379, 458
Twitch, single, 258
Tympanic canal, 302
Typhus, 405

Uintatheres, 506
Ulcer, stomach, 205
Ulna, 252
Ulothrix, 336
Umbilical arteries, 155
  cord, 355, 371
  vein, 155
Ungulates, 254, 506
Unguligrade, **254**
Uniformitarianism, **468**
Uranium, 486
Urea, 219, 242, 244
Ureter, 239
Urethra, 240, 348
Uric acid, 244
Urinary bladder, 240
Urine formation, 244
  substances in, 244
Urochorda, 562
Urochrome, 244
Urogenital system, 347
    female, 349
    male, 347
Uterus, 325, 350
Utricle, 306

Vaccine, **401**
Vacuole, contractile, 37, 94, 95, 245
  food, 37, 94, 99, 211
Vagina, 350
Vagus, 280
Valves of heart, 146
Variations, 413
Varicose veins, 165
Vas deferens, 348
  efferens, 348
Vascular bundles, 82
Veddoids, 544
Vein(s), 143
  blood flow in, 158
  umbilical, 155
  valves of, 144
  varicose, 165
Vegetal pole, 360
Vena cava, 146
Ventricle, 145, 374
Venus fly trap, 31, 32, 288
Vertebras, 252
Vertebrata, 118, 121, 562
Vestibular canal, 302
Vestigial organs, **509**, 510
Villi, 201
Viruses, filterable, 385, 390
Visceral mass, 113
Vision, 295
  defects in, 299
Visual purple, 224, 299
  violet, 299
Vital capacity, **179**
Vitalism, **28**
Vitamin(s), **221**
  A, 222
  B complex, 227
  B_1, 228
  B_2, 229
  B_6, 230
  B_{12}, 135, 230, 232
  C, 225
  D, 224
  E, 226
  G, 227, 229
  H, 227, 230
  K, 226
Vitreous humor, 297
Volvox, 96
Vomiting, 198
Vulva, 350

Wallace, A. R., 470
Wallace's Line, 518
Warning coloration, 550
Wassermann test, 407
Water in protoplasm, 22
  vascular system, 115
White race, 541
Womb, 350
Worm(s), acorn, 118
  guinea, 104
Worms, parasitic, 395
  proboscis, 103
  trichina, 104

Xerophthalmia, **224**
Xylem, 46, 171

Yolk, 425
  sac, 353

Zeuglodonts, 506
Zygote, **333**

CHECKED
2008

VERIFIED
2013

CFTRI-MYSORE
1490
Biology: Human a.

Acc No. 1490
Call No. G JO
VILLEE (CA)
OLOGY: